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Maternal Factors affect Individual and Population Level Morphometrics of Captive Male White-Tailed Deer (Odocoileus Virginianus)

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Maternal factors affect individual and population level morphometrics of captive male white-tailed deer (*Odocoileus virginianus*)

By

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Maternal factors have the potential to influence the morphometrics of offspring; however, the magnitude and persistence of those influences are not well known. I investigated the extent to which maternal factors influenced offspring phenotype at the individual and population level for captive white-tailed deer (*Odocoileus virginianus*) originating from three distinct physiographic regions of Mississippi, USA. First, I tested whether male white-tailed deer displayed improvements in weaponry and body size after two generations of being released from nutritional restrictions. I found that improved nutrition positively influenced all morphometrics; however, we observed variation in magnitude of improvement. Antler size was most responsive to improved nutrition while body mass and skeletal structures were less responsive; potentially indicating an adaptive strategy allowing males to increase yearly reproductive success without jeopardizing lifetime reproductive success. Second, we assessed whether maternal characteristics, early life characteristics or a combination of both persistently influenced morphometrics throughout maturity. I found that late birth date positively influenced offspring body mass through three-years of age; indicating that late-born fawns over-compensated for a

late start to life. I also identified an indirect silver-spoon effect as early-, heavy-born fawns were heavy juveniles. In turn, heavy juveniles were also heavy adults. Therefore, male white-tailed deer may gain reproductive opportunities by displaying one of two strategies to increase body mass. Lastly, I estimated heritability for six antler characteristics and quantified the influence of maternal factors such as parturition date and litter size on the predictability of antler size. All antler characteristics were highly heritable. Yearling antler size was a moderate predictor of antler size later in life, but accounting for maternal factors greatly improved predictability. The influence of maternal factors decreased with increasing male age suggesting that compensation for the negative influence of maternal factors may occur after an individual's first year of life. My results suggest that although antler characteristics are highly heritable, the large influence of maternal factors on predictability indicates that use of yearling antler size as selective harvest criteria may not achieve all management goals.

DEDICATION

I dedicate this dissertation to my family and friends who have supported me along the way. Although they did not always understand why I needed to move across the country to follow my dreams, they always supported me. There is no way I could have taken on this challenge without them.

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CHAPTER I

INTRODUCTION

There is still much to learn about how life history traits influence the ecology of a species. Life history theory explains how evolution designs organisms to achieve maximal reproductive success in the face of environmental problems (Stearns 2000). However, aspects of life history theory such as whether maternal characteristics persistently affects offspring phenotype or the ability of an individual to compensate for a poor start to life (e.g., late parturition date, increased neonatal competition, or nutritional stress) is poorly understood. These factors have the potential to greatly influence fitness. Therefore, my dissertation addressed these concepts related to life history theory using captive white-tailed deer (*Odocoileus virginianus*) as a model species.

The ability of white-tailed deer to compensate for small body morphometrics after being exposed to generations of nutritional stress is important to understanding white-tailed deer ecology. Nutrition can have profound implications on body and antler growth of white-tailed deer (French et al. 1956, Harmel et al. 1989). In Mississippi, there is variation in nutritional quality that is related to soil quality. Subsequently, the largest animals are generally associated with areas of highest quality nutrition (Strickland and Demarais 2000). Despite differences in antler size and body mass, smaller animals possess the ability to compensate when provided optimum nutrition. For example, Flinn (2010) reported partial compensation for antler size and body mass of captive male

white-tailed deer from low a quality soil region. However, Flinn (2010) only assessed 1 generation of males.

Future generations of males are needed to account for lagging maternal effects. Maternal effects can be defined as negative effects that occur in utero or during dependency as a response to environmental cues and can influence multiple generations of animals (Mech et al. 1991, Bernardo 1996, Freeman et al. 2013). However, optimum nutrition provided to animals for multiple generations can correct negative influences of maternal effects. For example, red deer displayed full compensation of morphometrics after multiple generations of improved nutrition (Vogt 1936, 1948, Beninde 1937, Frevert 1977; see Geist 1986, 1989). Studies involving multiple generations of white-tailed deer have also been conducted. Monteith et al. (2009) studied 2 generations of captive male white-tailed deer raised on optimum nutrition in South Dakota. However, Monteith et al. (2009) only observed partial compensation in antler score and body mass. Their results may, however, been influenced by low sample size. My first objective was to quantify the phenotypic improvement from first to second generation of captive male white-tailed deer raised on optimum nutrition.

Early life characteristics such as parturition date and litter size may influence fitness via effects on secondary sexual characteristics such as body mass. For example, late parturition date is known to have a negative influence on body mass for species such as white-tailed deer (Knox et al. 1991, Gray et al. 2002), bighorn sheep (*Ovis canadensis*; Feder et al. 2008), roe deer (*Capreolus capreolus*; Andersen and Linnell 1997), American bison (*Bison bison*; Green and Rothstein 1993), grasshopper mice (*Onychomys leucogaster;* Sikes 1998) and lesser scaup (*Aythya affinis*; Gurney et al. 2012). Similarly,

litter size is also known to negatively influence age-specific body mass of species including roe deer (Andersen and Linnell 1997), brown bears (*Ursus arctos*; Dahle et al. 2006), and polar bears (*Ursus maritimus*; Derocher and Stirling 1998). Although multiple studies have reported a negative relationship among body mass, parturition date, and litter size, Schultz and Johnson (1995) reported no relationship among these variables in male white-tailed deer. Understanding the effects of parturition date and litter size will allow managers to more fully understand factors that may influence growth of secondary sexual characteristics of white-tailed deer.

Maternal phenotype (i.e. body mass, age, and reproductive investment) may also influence offspring fitness. Larger mothers have a longer life expectancy, increased probability of reproduction and produce larger offspring with increased survival rates than smaller mothers (Verme 1989, Gaillard et al. 2000, Favre et al. 2008, and Hamel et al. 2009). Maternal phenotype also influences age of sexual maturity (Green and Rothstein 1991). Therefore, maternal phenotype influences offspring characteristics as well as maternal fitness. Maternal mass is also related to offspring body mass later in life. For instance, larger burying beetle (*Nicrophorus vespilloides*) mothers produced larger eggs and raised larger offspring compared to smaller mothers (Steiger 2013). The influence of maternal characteristics is important to offspring fitness and therefore examining the influence of maternal phenotype on offspring characteristics is warranted. My second objective assessed the influence of early life and/or maternal characteristics on secondary sexual characteristics of male white-tailed deer.

The ability to use yearling antler characteristics to predict future performance is important to managers. If future performance can be predicted then managers can

recommend selective harvest of younger animals that may not reach management goals. However, the level of heritability and predictability of antler characteristics must be established to enable managers to make scientifically based decisions.

Much work is still needed on estimating heritability (the relationship between breeding value and phenotype; Bourdon 2000) and predictability (the use of yearling antler size to predict antler size later in life) of antler characteristics for white-tailed deer. For instance, contradictory heritability estimates of antler characteristics for yearling white-tailed deer exist. Williams et al. (1994) reported that yearling antler characteristics were highly heritable whereas Lukefahr and Jacobson (1998) reported low to moderate heritabilities. More information is also needed on the use of yearling antler characteristics to predict future performance. Ott et al. (1997) and Lewis (2010) reported a positive relationship between yearling antler size and antler size at maturity. However, neither study accounted for potential confounding factors such as litter size and parturition date. My third objective addressed these issues by calculating heritability estimates for antler characteristics as well as quantified the influence of maternal factors on predictability of antler size.

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CHAPTER II

IMPROVED NUTRITION CUES SWITCH FROM MAINTENANCE TO DISPERSAL PHENOTYPES FOR MALE WHITE-TAILED DEER (*Odocoileus virginianus*)

2.1 Introduction

Environmental cues during gestation and lactation influence a wide variety of offspring phenotypic characteristics independent of an offspring's genotype (Mech et al. 1991, Bernardo 1996, Forchhammer et al. 2001, Freeman et al. 2013). Such environmental cues can also impact offspring stress levels, reproduction, immune system function (Triggs and Knell 2012, Bian et al. 2015), behavior and subsequent survival (Kerr et al. 2007, Skibiel et al. 2009, Storm and Lima 2010). Thus, spatial and temporal environmental variation may directly influence fitness of individuals as well as the dynamics of a population (Kruuk et al. 2000, McAdam et al. 2002, Räsänen and Kruuk 2007).

Environmental cues that influence the phenotype of future generations may alter the evolutionary trajectory of a population (McAdam et al. 2002, Räsänen and Kruuk 2007). For instance, when nutritional quality limits populations, individuals display a maintenance phenotype that promotes survival, but not the production of extravagant weaponry such as large antlers, horns and/or body sizes (Geist 1989). Conversely, a dispersal phenotype with larger weaponry and body sizes should be prevalent when nutritional resources are abundant. Maintenance and dispersal phenotypes may further

dichotomize because weaponry and body size influences reproduction (Clutton-Brock et al. 1982, Coltman et al. 2002, Festa-Bianchet 2012, Lidgard et al. 2012, Kie et al. 2013).

Populations of the same species display both maintenance and dispersal phenotypes which may have complicated historical morphometric-based taxonomy. For example, Strickland and Demarais (2000) reported a wide range in body and antler sizes of adult male white-tailed deer (*Odocoileus virginianus*) across Mississippi, USA, with some populations about one-third larger than others. This variation in phenotype is seemingly related to the variation in forage quality reported by Jones et al. (2008) with the largest males found in areas with the greatest quantity and quality of forages. However, genetic bottlenecks, founder effects or genetic remnants from white-tailed deer restoration (DeYoung et al. 2003, Sumners et al. 2015) could be partially responsible for some of the observed phenotypic variation. Some findings of Strickland and Demarais (2000) support the subspecies classification of white-tailed deer in southeastern Mississippi (*O. v. osceola*; Baker 1984), which was based on phenotypic size (Barbour and Allen 1922). However, this subspecies classification may be unnecessary if differences between the populations are not due to genetic differences and are compensated for after improvement of nutritional resources. Increases in weaponry and body mass as a response to improved nutrition has been reported for some ungulates (red deer; *Cervus elepha us,* roe deer; *Capreolus capreolus*; reviewed in Geist 1986, white-tailed deer, Monteith et al. 2009); however, the magnitude and number of generations required for phenotypic change once nutritional limitations are relieved is still in question.

Our goal was to measure phenotypic change as a response to improved nutrition during two generations using captive, male white-tailed deer. We hypothesized that a high-quality diet (i.e., 20% crude protein deer pellets fed *ad libitum*) would increase size of phenotypic characteristics for captive male white-tailed deer by alleviating potential lagging maternal effects due to nutritional restrictions experienced in the wild (Geist 1986, Monteith et al. 2009). We also hypothesized that regional compensation of phenotypic characteristics would occur in the second generation (Monteith et al. 2009). We further hypothesized that not all phenotypic characteristics would respond to improved nutrition at the same rate or magnitude. For example, skeletal structures seemingly display a high level of canalization (i.e., the ability to produce the same phenotype regardless of environment; Waddington 1957, Simard et al. 2008) and may not respond to improved nutrition. However, weaponry and body mass is known to influence reproduction positively (Clutton-Brock et al. 1982, Coltman et al. 2002, Bartoš and Bahbouh 2006), and such, should display larger increases than skeletal structures when quality nutrition is abundant. Therefore, I predicted antler size and body mass would display a larger increase compared to skeletal structures. Alternatively, phenotype could be limited by population-level genetics that limit the response to improved nutrition within one generation.

2.2 Materials and Methods

2.2.1 Source Populations

To incorporate the range of inherent genetic and habitat variation, we captured deer from 29 sites located on public wildlife management areas and private lands that were part of the Deer Management Assistance Program (Guynn et al. 1983) throughout 3

soil source regions in Mississippi, USA (Figure 2.1). The Delta soil region comprises nearly 14% of total land area of Mississippi, USA, and is classified as a high quality soil region with agriculture as the primary land use (e.g., cotton, soybean, corn, rice; Pettry 1977, Snipes et al. 2005). The mean soil productivity value for capture sites in the Delta region was (10.1, range 0–19; Soil Drainage and Productivity Index Map, http://foresthealth.fs.usda.gov/soils/PIMap). The Delta soil region and all study animal source populations were within the distribution of *O. v. virginianus* (Baker 1984). The Thin Loess soil region (upper and lower Thin Loess combined) comprises almost 14% of total land area of Mississippi, USA, and is considered a medium quality soil region. Its primary land use is also agriculture, though not to the same extent as in the Delta (Pettry 1977, Snipes et al. 2005). The mean soil productivity value for capture sites in the Thin Loess region was (8.8, range 0–19; Soil Drainage and Productivity Index Map, http://foresthealth.fs.usda.gov/soils/PIMap). The Thin Loess region and all study animal source populations were within the distribution of *O. v. virginianus* (Baker 1984). Lastly, the Lower Coastal Plain (LCP) soil region comprises nearly 22% of Mississippi. This area is classified as a low quality soil region and has leaching issues, limiting most land uses to pine (*Pinus* spp.) production and livestock grazing (Pettry 1977, Snipes et al. 2005). The mean soil productivity value for capture sites in the LCP region was (3.7, range 0–19; Soil Drainage and Productivity Index Map, http://foresthealth.fs.usda.gov/soils/PIMap). The LCP soil region overlaps the geographical distribution of *O. v. osceola* and four of the six study animal source populations were in or within 21 km of this distribution (Baker 1984). This subspecies was described as being smaller than *O. v. virginianus* (Barbour and Allen 1922).

2.2.2 Study Area

We brought all wild caught animals back to the Mississippi State University Rusty Dawkins Memorial Deer Unit (MSU Deer Unit). The MSU Deer Unit is located in Oktibbeha County, Mississippi, USA, and is subdivided into 5 0.4–0.8 ha pens. We housed ≥ 5.5-month-old males at satellite facilities located near Macon, Noxubee County; Kosciusko, Attala County; Utica, Copiah County; and Morton, Scott County, Mississippi, USA. Each satellite facility consisted of 2 0.7-ha pens. We raised all deer on a high-quality diet comprised of 20% crude protein deer pellets (Purina AntlerMax Professional High Energy Breeder 59UB, Purina, St. Louis, MO) fed *ad libitum*. Available forages within pens included Durana Clover and Max-Q Fescue (Pennington Seed Co., Madison, GA) along with volunteer grasses and forbs. All facilities had similar husbandry practices.

2.2.3 First and Second Generations

We produced 2 generations of offspring by allowing first-generation males to naturally breed first generation females from the same soil source region (e.g., Delta males bred Delta females, Thin Loess males bred Thin Loess females and LCP males bred LCP females). Each year we placed two males with 7–16 females, for an average breeding sex ratio of 1 male per 8 females. Females produced offspring for multiple years but typically with different sires each year. First generation (F1) deer were either wild caught 5.5-month old fawns or offspring of wild born deer and were raised on a high-quality diet *ad libitum* the remainder of the project. Second generation (F2) deer were offspring of F1 deer, were raised in captivity from birth and had access to the same high-quality diet *ad libitum* as their F1 parents.

2.3 Data Collection

2.3.1 Newborn fawns

We searched the MSU Deer Unit daily for fawns starting on 1 June from 2005 to 2010. We uniquely marked fawns within 1 day of birth with medium plastic ear tags (Allflex, Dallas, Texas, USA), measured body mass (nearest 0.01 kg) using a digital vertical hanging scale (Pelouze, Bridgeview, Illinois, USA), measured total body length and hind food length to the nearest mm and collected hair samples or ear notches for DNA analysis. DNA Solutions (Oklahoma City, Oklahoma, USA) assigned parentage of fawns using DNA based on a proprietary, non-statistical custom structured query language database known as the DNA Solutions Animal Solutions Manager (DASM©). In the pairwise allele comparison DNA Solutions assigned parentage when they excluded all but 1 sire and 1 dam based upon a shared allele from each parent at all loci tested (B. G. Cassidy, DNA Solutions, personal communication). We administered 2 cc's of Clostridium Perfringens types C and D Toxoid Essential 3 and Clostridium Perfringens Types C and D Antitoxin Equine Origin (Colorado Serum Company, Denver, Colorado, USA) subcutaneously, and 0.3 cc/kg of Ivermectin in Propylene Glycol (Mississippi State University Veterinarian School, Mississippi State, Mississippi, USA) orally to each fawn.

2.3.2 Juveniles

We chemically immobilized juveniles approximately 5.5-months after their average region-specific birth date. We used a 2:1 mixture of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and xylazine HCl (Phoenix Scientific, St.Joseph, Missouri, USA) with an approximate dosage of 6.6 mg/kg via cartridge-fired dart (Pneu-Dart Inc, Williamsport, Pennsylvania, USA). We recorded the same measurements for

juveniles that we collected from new born fawns, marked juveniles with a large plastic tag in each ear (Allflex, Dallas, TX) and administered size-appropriate amounts of the antibiotic Nuflor ™ (Schuering-Plough Animal Health Corp., Summit, NJ), the endectocide Ivermectin (Norbrook Laboratories, LTD., Down, Northern Ireland, UK), the clostidrial vaccine Vision 7 with SPUR (Ivesco LLC, Iowa Falls, IA) and the leptospirosis vaccine Leptoferm-5 (Pfizer, Inc., New York, NY). We reversed the effects of xylazine HCl with 0.125 mg/kg yohimbine HCl (Kreeger 1996) or 4.0 mg/kg tolazoline HCl (Miller et al. 2004). We then transported the approximately 5.5-month-old males to 1 of 4 satellite facilities. Each satellite facility received an equal, random sample of fawns from each soil source region.

2.3.3 Adults

We chemically immobilized adult males (≥ 1 year-old) for data collection during October and November, 2005–2010. We repeated the same prophylactics and morphometric measurements collected from neonates and juveniles. We also measured antler size of adult males by measuring the inside spread, basal circumference and beam length of antlers prior to their removal. We removed antlers approximately 3 cm above the burr with a reciprocating saw or diamond wire but did not remove antlers less than 3 cm long. We weighed antlers to the nearest 0.1 g and assigned a minimal critical antler mass of 1 g for first-year animals with antlers shorter than 3 cm. We calculated an antler score similar to the gross non-typical Boone and Crockett score (Nesbitt et al. 2009), but measured less than 4 circumferences when antlers contained less than 3 tines. For example, a main beam with 2 typical points included only 3 circumference measurements. We also included body mass and antler score from individuals harvested

from Mississippi, USA as reference points. We calculated an estimated live weight of individuals by multiplying the eviscerated body mass reported by Strickland and Demarais (2000) by 1.285. We used antler measurements used by Strickland and Demarais (2000) to calculate an antler score index to derive mean, 3.5-year-old antler scores for each regional population by applying those measurements to a predictive equation (Strickland et al. 2013). The Mississippi State University Institutional Animal Care and Use Committee approved all capture, handling, and marking techniques under protocols 04–068, 07–036, 10–033 and 13–034.

2.3.4 Data Analysis

We used an animal model within the Monte Carlo Markov Chain generalized linear mixed model (MCMCglmm) framework in the MCMCglmm package in Program R (R Development Core Team 2008, version 3.1.3; Hadfield 2010) to estimate the influence of long-term, high-quality nutrition on male white-tailed deer phenotype. Using an animal model allowed us to account for any variation in phenotype related to the sire and dam. We also included the animal ID as a random effect, which accounted for multiple measurements of each individual. Body mass and antler size varies by the soil region where we obtained our source populations (Strickland and Demarais 2000), so we included soil source region as a fixed effect. Body mass and antler size are known to increase with age so we also included age as a fixed effect. Examining the interaction between generation and age would have been informative, but sample size varied for each generation, region and age class and was inadequate to assess this interaction (Table 2.1). We concluded that fixed effects were significant in each analysis if the 95% Credible Intervals *(95% CI)* did not overlap 0. For each model, we ran 2 chains with uninformative

priors and 100,000 iterations for each chain. We sampled every 10th iteration after a 50,000 iteration burn-in period. We examined trace plots for convergence of each variable as well as for convergence between chains. We confirmed there was no autocorrelations between iterations within each model. We then used the model parameters to predict means for each response variable (i.e., body mass, total body length, hind foot length, antler size and antler mass) using the MCMCglmm.predict function in Program R.

2.4 Results

All phenotypic characteristics increased in size from first to second generation. Quality long-term nutrition (as represented by our generation variable) positively influenced phenotype (range β = 5.51–88.62, range *95% CI* = 0.73–152.21; Table 2.2; Figures 2.2, 2.3). Age also positively affected phenotype (range β = 8.62–351.53, range *95% CI* = 7.44–370.95; Table 2.2).

Although all phenotypic characteristics increased in size after two generations of improved nutrition, there was still regional variation among populations for some characteristics (Table 2.2; Figure 2.2). Soil source region was a significant predictor for body mass (range β = -13.80 – -11.06, range *95% CI* = -19.54 – -5.45) and both skeletal measurements (range β = -116.52 – -22.50, range *95% CI* = -162.65 – -13.16) indicating that Delta males grew larger bodies than Thin Loess and LCP males. However, soil source region was not a significant predictor for antler score or antler mass (range β = -83.33 – -6.00, range *95% CI* = -182.18 – -107.42), which suggests there was no longer regional variation for these variables after two generations of improved nutrition.

We observed variation in the magnitude of increase for phenotypic characteristics. For example, antler size and mass were generally more sensitive to improved nutrition compared to body mass and skeletal size. Antler mass increased 2.5 times more than body mass and about 15 times more than total body length (Table 2.3) for Thin Loess males. Males from the other regional populations displayed similar increases from first to second generation for each phenotypic characteristic.

Magnitude of generational improvement also varied among regional populations. Males from the LCP regional population increased most, as they displayed up to a 2 times larger increase from first to second generation compared to the Delta and up to a 5 times larger increase compared to the Thin Loess regional populations (Table 2.3). LCP males displayed a 15-25% increase in body mass, antler score and antler mass from first to second generation, while Delta and Thin Loess males increased only 7-14% and 5-13%, respectively (Table 2.3). Total body length and hind foot length followed similar patterns of increase as LCP males displayed about a 3-4% increase from first to second generation while Delta males displayed about a 1-2% increase and Thin Loess males displayed about a 1% increase. We found similar patterns when examining changes in body mass and antler score from harvested to second generation individuals. LCP males increased body mass and antler score about 24 and 38%, respectively (Table 2.4). Thin Loess males displayed about a 10 and 16% increase and Delta males displayed about an 11 and 5% increase for body mass and antler score, respectively.

2.5 Discussion

Our results support our hypothesis that high-quality nutrition would positively influence the phenotype of captive male white-tailed deer. In addition to influencing

phenotypic characteristics for several species (e.g., tarsus length of *Larus michahellis*, Saino et al. 2010; body size of *Liasis fuscus,* Madsen and Shine 2004; body mass of *Ursus americanus*, *Ursus arctos*, Welch et al. 1997, and *Cervus candensis*, Cook et al. 2004; antler mass of *Odocoileus hemionus*, Robinette et al. 1973), nutrition also influences other characteristics (reviewed in Parker et al. 2009). For example, nutrition influences hormone levels (Taillon and Côté 2008; Bryan et al. 2013) and social behaviors such as dominance (discussed in Michel et al. 2016) and aggressiveness (Taillon and Côté 2007, Robbins 2008). Understanding how nutrition influences these characteristics allows for a better understanding of how populations adapt to their environment as nutrition ultimately affects survival (Côté and Festa-Bianchet 2001, Cook et al. 2004, Lomas and Bender 2007).

Nutritional cues that positively or negatively affect offspring while in utero or during dependency are generally referred to as maternal effects (Bernardo 1996). Maternal effects can be thought of as a mother "communicating" the environment with her offspring. This "communication" allows for offspring to display a phenotype suitable for the environment they are born into when the environment is predictable (Mousseau and Fox 1998). By providing high-quality nutrition *ad libitum* we simulated a predictable, high-quality environment allowing offspring to display a phenotype consistent with their maternal environment. Our generational improvements support previous studies of long-lived ungulates (red and roe deer, reviewed in Geist 1986; white-tailed deer, Monteith et al. 2009) and suggest that ungulates are capable of switching from maintenance to dispersal phenotypes within an ecological timeframe. This phenotypic plasticity,

potentially mediated by maternal effects, likely explains the widespread distribution of whitetails across the New World (discussed in Wolverton et al. 2009).

Epigenetic changes, the heritable changes in gene expression and function that cannot be explained by changes in DNA sequence (Richards 2006, Bird 2007, Bossdorf et al. 2008), are a likely mechanism for maternal effects. Simply put, epigenetic variation can be directly influenced by the environment, thus influencing an individual's phenotype and may be inherited by future generations (Bossdorf et al. 2008, Powledge 2011). For example, in lab mice, maternal diet influenced offspring phenotypes such as coat color (Wolff et al. 1998, Waterland and Jirtle 2003) and tail straightness (Waterland et al. 2006). Epigenetics are important because they explain some heritable phenotypic variation in natural populations that are not explained by differences in DNA sequence (Bossdorf et al. 2008) and may provide insight into the phenotypic plasticity of animals (Bossdorf et al. 2008). We hypothesize white-tailed deer phenotypes are influenced by epigenetic processes.

Our results also suggest that phenotypic-based subspecies classification may be inappropriate for Mississippi white-tailed deer. The dramatic increase in antler and body size that we report for the LCP regional population suggests that phenotype may not be restricted by genetics, but phenotypic differences between *O. v. virginianus* and *O. v. osceola* may instead be related to environmental differences. This further supports the results of DeYoung et al. (2003) who found no genetic differences among white-tailed deer subspecies in Mississippi. Therefore, caution should be used when using subspecies classifications for Mississippi white-tailed deer (Geist 1989).

We found partial support of our hypothesis that we would observe regional compensation for all phenotypic characteristics. Body mass and skeletal measurements were greatest for Delta males but did not differ between Thin Loess and LCP males. This supports Monteith et al. (2009) who found that body mass still varied after two generations of improved nutrition between two populations of white-tailed deer originating from South Dakota, USA. There are 2 possible explanations for this result. First, these differences may indicate possible genetic differences among populations that cannot be overcome by improving nutritional quality and quantity. Second, more than 2 generations of improved nutrition may be needed for full regional compensation to be displayed. Geist (1986) suggested that up to 4 generations of improved nutrition may be needed for white-tailed deer to display their full genetic potential. However, antler score and antler mass did not vary among regional populations after 2 generations of improved nutrition. This result supports previous research of ungulates (reviewed in Geist 1986, Monteith et al. 2009) and suggests antler size variation among harvested populations is due to regional variation in nutritional quantity and quality (Jones et al. 2008, 2010) as well as regional variation in land-use (Strickland and Demarais 2008). Regional variation of body, but not antler characteristics, may also indicate differences in plasticity of white-tailed deer phenotype once quality nutrition is available.

Our results support our prediction that magnitude of change would vary among phenotypic characteristics as we identified a clear hierarchy of growth prioritization. Antler mass displayed the largest increases followed by antler score, body mass and finally skeletal characteristics. Prioritization of antler mass suggests that individuals allocate nutritional resources towards increasing antler strength over antler size.

Increased antler mass reduces the probability of antlers breaking (Landete-Castillejos et al. 2010) and could therefore increase access to mates compared to antler size alone as a visual indicator of male quality (reviewed in Demarais and Strickland 2011). Concomitantly, these differential rates of change suggest skeletal characteristics display a greater level of canalization than weaponry and body mass. For example, skeletal characteristics displayed minimal change ($\leq$ 3.9%) from first to second generation though antler and body mass increased up to about 25 and 15%, respectively. These results are similar to Simard et al. (2008) who found white-tailed deer body mass decreased with a decline in nutritional quality, but hind foot length did not change. Therefore, skeletal structures are likely highly prioritized during growth and display a consistent size regardless of the nutritional environment an individual experiences (Geist 1989).

Different levels of canalization among phenotypic characteristics are a potential adaptation to increase male reproductive success (Geist 1989, Kruuk et al. 2002). Weaponry and body mass are known to influence access to mates (Clutton-Brock et al. 1982, Festa-Bianchet et al. 2012). Antlers are cast and regrown on a yearly basis (Demarais and Strickland 2011); thus, increasing antler mass and size within a given year when nutritional quality allows for it may improve access to mates without having to expend resources producing large antlers in subsequent years if resources are limited. However, body mass is less sensitive to changes in the environment in comparison to antler characteristics, and thus more easily reproducible. Therefore, increases in weaponry is advantageous when resources are abundant, but not necessarily when resources are limited (Geist 1989). These adaptations could potentially allow for an

individual to increase yearly reproductive success without jeopardizing long-term reproductive success; however, future studies are needed to assess these relationships.

Regional variation in phenotypic change is not explained by differences in nutritional quality experienced in the wild. The greater phenotypic improvement by the LCP regional population is intuitive, as deer from this region experienced a greater nutritional limitation in the wild compared to the Delta and Thin Loess regional populations (Jones et al. 2008). However, phenotypic improvements for the Delta regional population were unexpected. Deer from the Delta regional population display larger phenotypic characteristics in the wild compared to deer from the Thin Loess and LCP regional populations (Strickland and Demarais 2000). Deer from the Delta regional population also benefit from high-quality natural forages (Jones et al. 2008, 2010) and land-use practices that further promote additional high-quality forage production (i.e., agriculture; Strickland and Demarais 2008). However, the increased body mass and antler size for the Delta regional population indicates that nutritional quality and/or quantity is lacking in the wild. Therefore, caution must be used when assessing nutritional quality as populations may benefit from improved nutrition even when nutrition appears to be adequate.

2.6 Conclusion

Our results show that nutritional improvements cue a switch from maintenance to dispersal phenotypes for a long-lived mammal. This switch in phenotype may influence the evolutionary trajectory of a population, as males with the largest antlers and heaviest body masses may breed more than those with smaller antlers and lighter body masses. If so, this would promote increases in antler and body size, as these are heritable traits

(Réale et al. 1999, Kruuk et al. 2002, Michel et al. *In prep*). We report drastic phenotypic increases after two generations of improved nutrition, which suggests that a potential shift in evolutionary trajectory may occur on an ecological time scale. Therefore, evaluating past and present nutritional environments is essential when assessing phenotypic variation as past environments influence current phenotypes.

Table 2.1 Sample sizes for captive male white-tailed deer from three regional soil source populations spanning two generations.

Variable	Delta		Thin Loess		LCP	
	F1 (n)	F2 (n)	F1 (n)	F2 (n)	F1 (n)	F2 (n)
1.5 years						
Body Mass (kg)	22	18	17	25	27	18
Antler Score (cm)	22	19	17	25	27	18
Antler Mass (g)	22	19	17	25	27	18
Hind Foot Length (mm)	22	18	17	25	27	18
Total Body Length (mm)	22	18	17	25	27	18
2.5 years						
Body Mass (kg)	19	16	15	23	25	16
Antler Score (cm)	19	16	15	23	25	16
Antler Mass (g)	19	16	15	23	23	16
Hind Foot Length (mm)	19	16	15	23	25	16
Total Body Length (mm)	19	16	15	23	25	16
3.5 years						
Body Mass (kg)	15	15	14	19	21	11
Antler Score (cm)	15	15	14	21	22	11
Antler Mass (g)	15	15	14	21	22	11
Hind Foot Length (mm)	15	15	14	21	22	11
Total Body Length (mm)	15	15	14	20	22	11

Table 2.2 Sample sizes for captive male white-tailed deer from three regional soil source populations spanning two generations.

Variable	Delta		Thin Loess		LCP	
	F1 (n)	F2 (n)	F1 (n)	F2 (n)	F1 (n)	F2 (n)
1.5 years						
Body Mass (kg)	22	18	17	25	27	18
Antler Score (cm)	22	19	17	25	27	18
Antler Mass (g)	22	19	17	25	27	18
Hind Foot Length (mm)	22	18	17	25	27	18
Total Body Length (mm)	22	18	17	25	27	18
2.5 years						
Body Mass (kg)	19	16	15	23	25	16
Antler Score (cm)	19	16	15	23	25	16
Antler Mass (g)	19	16	15	23	23	16
Hind Foot Length (mm)	19	16	15	23	25	16
Total Body Length (mm)	19	16	15	23	25	16
3.5 years						
Body Mass (kg)	15	15	14	19	21	11
Antler Score (cm)	15	15	14	21	22	11
Antler Mass (g)	15	15	14	21	22	11
Hind Foot Length (mm)	15	15	14	21	22	11
Total Body Length (mm)	15	15	14	20	22	11

Table 2.3 Summary of the MCMCglmm models describing the influence of generation (F2), age and region (regionLoess, regionLCP) on morphometric variables.

	Response Variable									
	Body Mass		Hind Foot Length		Total Body Length		Antler Score		Antler Mass	
	Beta	95% CI	Beta	95% CI	Beta	95% CI	Beta	95% CI	Beta	95% CI
Intercept	42.04	37.89 – 46.61	428.22	421.07 - 435.78	1601.74	1563.45 - 1636.56	-5.44	-26.14 - 15.84	-263.69	-344.23 - -19.45
F2	5.51	1.90 – 9.17	6.84	0.73 - 13.05	33.66	0.89 - 62.88	20.00	2.09 - 37.14	88.62	17.49 - 152.21
Age	15.24	14.60 – 16.18	8.62	7.44 - 9.80	91.97	84.99 - 98.57	95.28	90.63 - 99.61	351.53	332.13 - 370.95
regionLCP	-13.80	-19.54 - -8.34	-23.80	-33.28 - -14.39	-116.52	-162.65 - -69.25	-9.55	-34.16 - 16.26	-83.33	-182.18 - 16.16
regionLoess	-11.06	-16.43 - -5.45	-22.50	-31.71 - -13.16	-109.52	-153.09 - -62.14	-1.88	-27.23-22.32	6.00	-84.96 - 107.42

We coded generation and region as categorical variables and age as a continuous variable. The intercept represents first generation (F1), one-year-old Delta males and is considered a reference term for comparison of generation, age and regional soil source population.

Table 2.4 Percent increase in morphometrics from first to second generation of captive 3.5-year-old male white-tailed deer housed in Noxubee, Attala, Copiah, and Scott County, Mississippi, USA.

Variable	Delta			Thin Loess			LCP		
	F1 Mean	F2 Mean	% Increase	F1 Mean	F2 Mean	% Increase	F1 Mean	F2 Mean	% Increase
Body Mass (kg)	88.3	94.2	6.6	80.5	84.5	5.0	71.0	81.4	14.6
Total Body Length (mm)	1879.8	1914.0	1.8	1799.7	1815.0	0.8	1734.6	1803.7	3.9
Hind Foot Length (mm)	456.5	462.4	1.2	437.8	441.8	0.9	426.4	438.0	2.7
Antler Score (cm)	277.6	301.0	8.4	294.2	306.2	4.0	258.0	308.7	19.6
Antler Mass (g)	777.8	886.9	14.0	818.0	922.5	12.7	673.4	844.4	25.3

Table 2.5 Percent increase in body mass and antler size from 3.5-year-old male white-tailed deer harvested in Mississippi, USA to a second generation of captive 3.5-year-old male white-tailed deer housed in Noxubee, Attala, Copiah, and Scott County, Mississippi, USA and raised on optimum nutrition.

Variable	Delta			Thin Loess			LCP		
	Harvest Mean	F2 Mean	% Increase	Harvest Mean	F2 Mean	% Increase	Harvest Mean	F2 Mean	% Increase
Body Mass (kg)	85.1	94.2	10.7	76.6	84.5	10.3	65.5	81.4	24.2
Antler Score (cm)	287.8	301.0	4.5	263.4	306.2	16.2	224.2	308.8	37.6

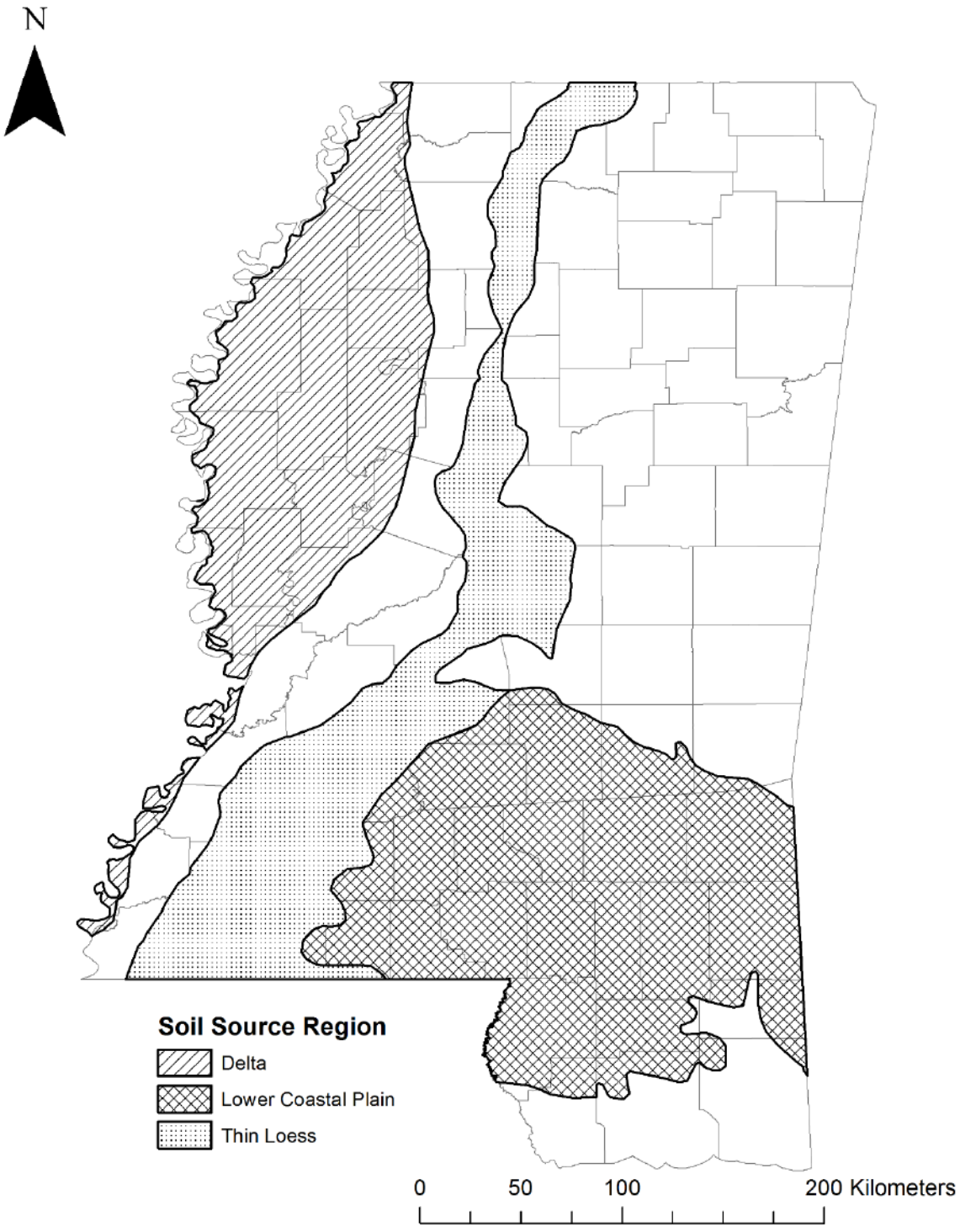

Figure 2.1 Physiographic regions of Mississippi where pregnant dams and fawns were captured.

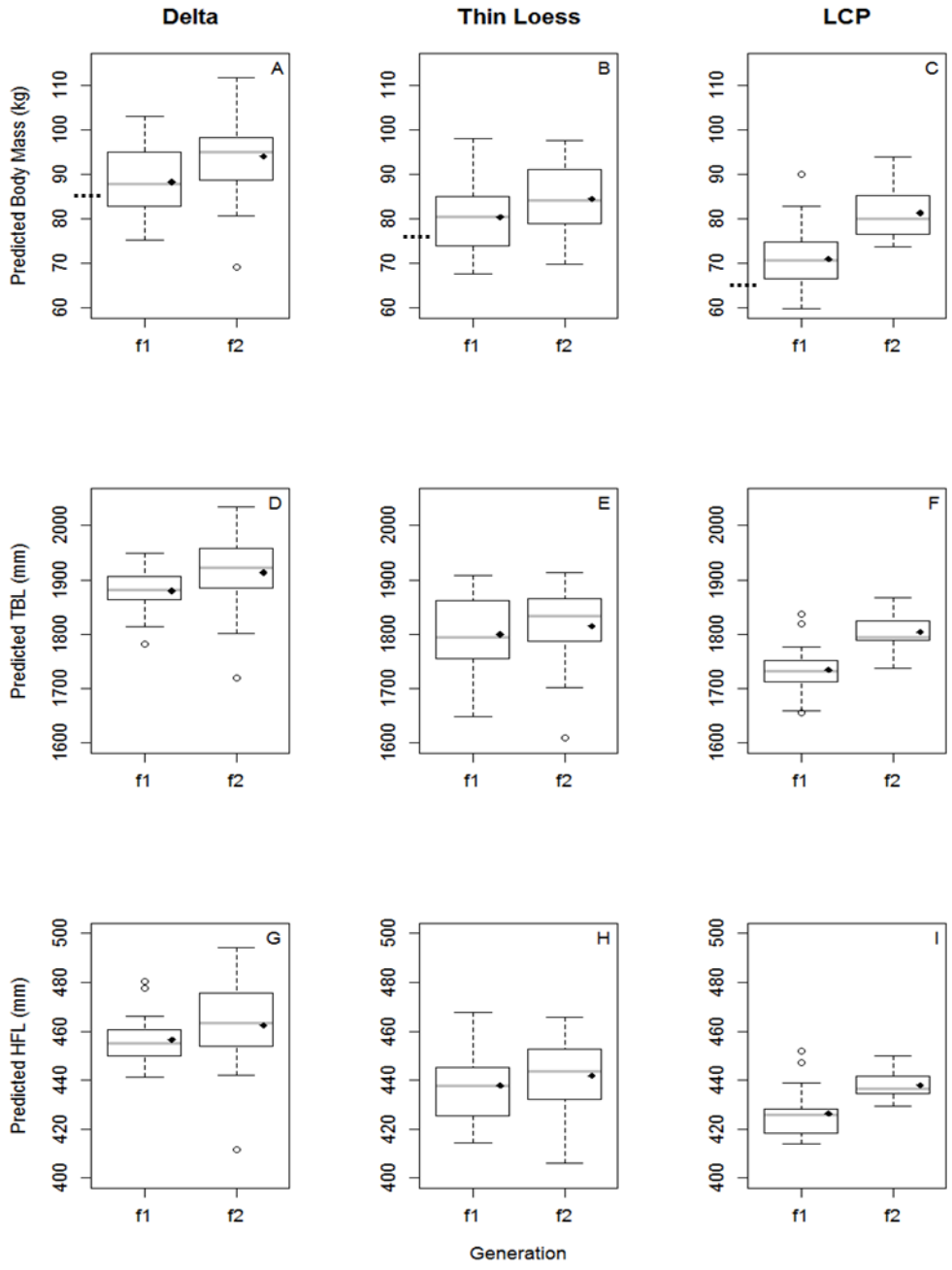

Figure 2.2 Generational improvement of median body morphometrics for captive 3.5-year-old male white-tailed deer housed in Noxubee, Attala, Copiah, and Scott County, Mississippi, USA.

Dashed line on the y-axis represents mean body mass of harvest data collected from Mississippi, USA and is used for comparison to first and second generations. The black diamond represents the predicted mean. Whiskers indicate minimum and maximum values while open circles indicate outliers.

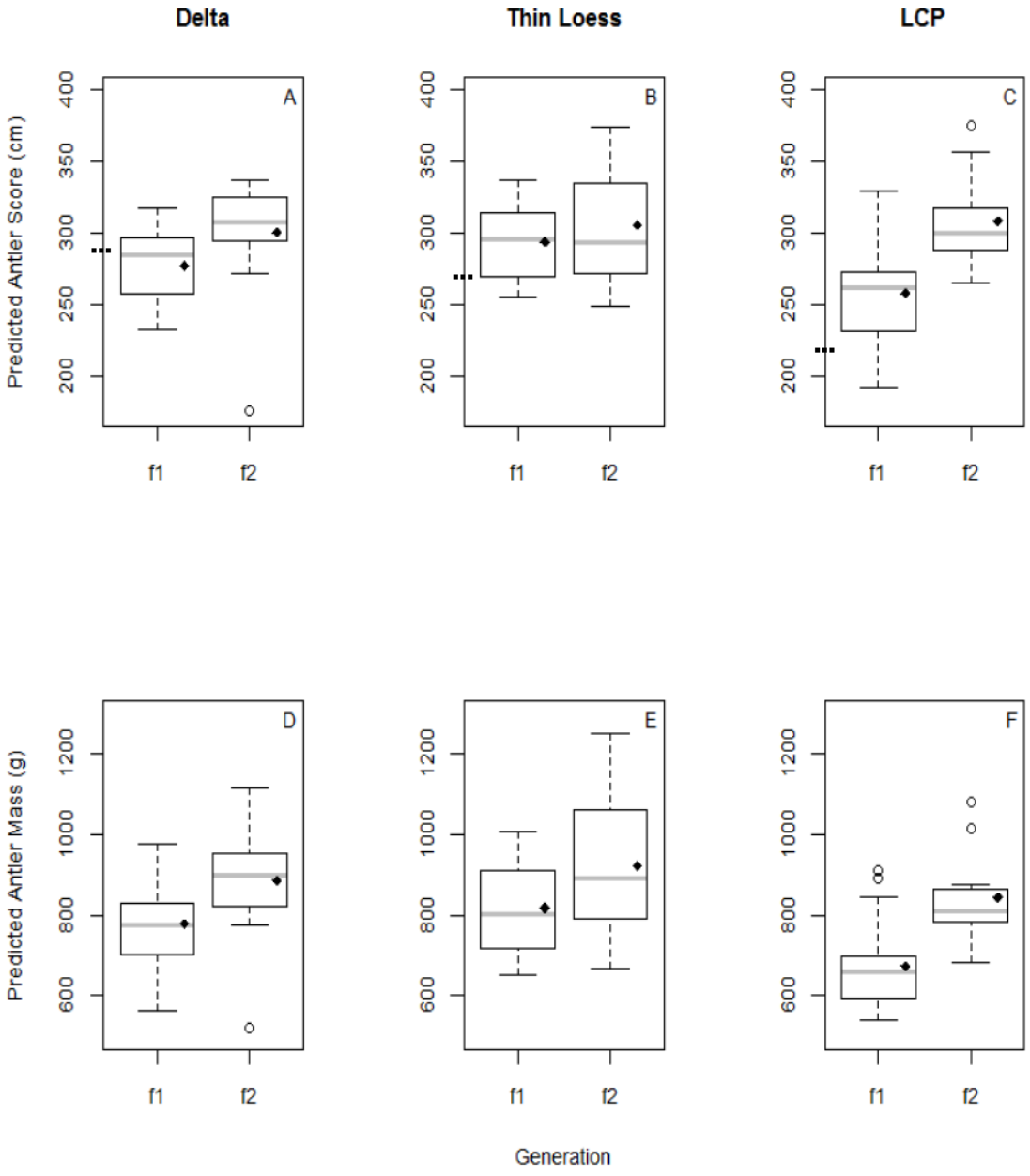

Figure 2.3 Generational improvement of median antler characteristics for captive 3.5-year-old male white-tailed deer housed in Noxubee, Attala, Copiah, and Scott County, Mississippi, USA.

Dashed line on the y-axis represents mean antler score of harvest data collected from Mississippi, USA and is used for comparison to first and second generations. The black diamond represents the predicted mean. Whiskers indicate minimum and maximum values while open circles indicate outliers.

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CHAPTER III

OVER-COMPENSATION OF BODY MASS IN RESPONSE TO LATE BIRTH DATE IN A LONG LIVED UNGULATE

3.1 Introduction

Life history theory explains how evolution designs organisms to achieve optimal reproductive success in the face of environmental problems (Stearns 2000). Reproduction can also be influenced by maternal effects (which occur in utero or during dependency as a response to environmental cues; Bernardo 1996) because they influence secondary sexual characteristics at the population level (Monteith et al. 2009). Maternal effects are important because they influence individual fitness (Kruuk et al. 2000) as well as the evolutionary trajectory of a population (McAdam et al. 2002, Räsänen and Kruuk 2007).

Although previous research suggests that maternal effects influence offspring phenotype at the population level, less is known about persistence of specific maternal and/or early life characteristics. Maternal age and maternal body mass influence offspring phenotype because younger mothers are generally lighter and less capable than older mothers (Festa-Bianchet et al. 1995, Ditchkoff 2011). Previous year reproductive success may also influence offspring phenotype by influencing current year maternal body condition (Clutton-Brock et al. 1982, Monteith et al. 2013, Strickland et al. 2008). Similarly, early life characteristics such as birth date influence offspring phenotype; early-born individuals are generally heavier at weaning than late-born individuals born in

the same year (Green and Rothstein 1993, Côté and Festa-Bianchet 2001, Feder et al. 2008). Such influences are assumed to persist throughout maturity; offspring birth mass is associated positively with mature body mass (Schultz and Johnson 1995, Cook et al. 2004, Michel et al. 2015), but these types of analyses are limited by the challenge of assigning maternity and collecting life-long data. Nevertheless, maternal characteristics that influence offspring phenotype may directly affect offspring reproductive success which impacts the mother's fitness (reviewed in Hewison and Gaillard 1999).

Secondary sexual characteristics such as body mass and antler and horn size positively influence reproductive success in a range of taxa, including ungulates (*Cervus elaphus*; Clutton-Brock et al. 1982, *Ovis canadensis*; Festa-Bianchet et al. 2000, *Ovis aries*; Robinson et al. 2006), pinnipeds (*Mirounga angustirostris*; Crocker et al. 2012) and canids (*Vulpes vulpes*; Iossa et al. 2008). Thus, compensatory growth of secondary sexual characteristics would be beneficial for individuals who experience a poor start to life. Compensatory growth in response to release from early life nutritional constraints has been documented for a range of taxa (reviewed in Hector and Nakagaw 2012); however, compensatory growth in response to a late start to life (late birth date) has been documented rarely (Orizaola et al. 2010, Stier et al. 2014). Additionally, few studies have assessed the persistence of these effects through maturity (Green and Rothstein 1993).

Our objective was to determine the extent to which maternal and early life characteristics contribute to variation in body mass and antler size of a long-lived mammal. We assessed if offspring phenotypic impacts persisted throughout maturity or if offspring displayed the ability to compensate for a poor start to life in captive male white-tailed deer (*Odocoileus virginianus*).

We developed models representing four hypotheses to assess how maternal and early life characteristics might influence body mass and antler size of captive male white-tailed deer through maturity. Our "direct maternal characteristics" hypothesis (DM; Figure 3.1A) represents only maternal age, maternal body mass and previous year cumulative lactation demand having direct effects on offspring body mass and antler size through three-years of age. We categorized deer as mature at three-years of age as epiphyseal plate growth has ceased (Flinn et al. 2013) and more than 90% of maximum body mass has been attained (Strickland and Demarais 2000). Our "direct early life characteristics" hypothesis (DEL; Figure 3.1B) represents only birth date directly affecting offspring phenotype through three-years of age. Our "direct maternal and early life characteristics" hypothesis (DMEL; Figure 3.1C) represents maternal and early life characteristics directly influencing offspring body mass and antler size through three-years of age. Finally, our "indirect maternal and early life characteristics" hypothesis (IMEL; Figure 3.1D) represents maternal and early life characteristics that indirectly influence offspring phenotype through their relationships with offspring birth mass and juvenile body mass through three-years of age.

3.2 Materials and Methods

3.2.1 Study Area

We housed all study animals in captivity and reared them under similar husbandry practices. Mississippi State University Rusty Dawkins Memorial Deer Unit (MSU Deer Unit) is located in Oktibbeha county, Mississippi, USA, and is subdivided into 5 0.4–0.8 ha pens. We housed ≥ 5.5-month-old males at satellite facilities located near Macon, Noxubee County; Kosciusko, Attala County; Utica, Copiah County; and Morton, Scott

County, Mississippi, USA. Each satellite facility consisted of 2 0.7-ha pens. We raised all deer on a high-quality diet comprised of 20% crude protein deer pellets (Purina AntlerMax Professional High Energy Breeder 59UB, Purina, St. Louis, MO) fed *ad libitum*. Available forages within pens included Durana Clover and Max-Q Fescue (Pennington Seed Co., Madison, GA) along with volunteer grasses and forbs.

3.2.2 Data Collection

We chemically immobilized adult females (≥ one-year-old) for data collection during November, 2006–2010. We used a 2:1 mixture of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and xylazine HCl (Phoenix Scientific, St. Joseph, Missouri, USA) with a dosage of 6.6 mg/kg via cartridge-fired dart (Pneu-Dart Inc., Williamsport, Pennsylvania, USA). Once sedated, we measured body mass and administered size-appropriate amounts of the antibiotic Nuflor ™ (Schuering-Plough Animal Health Corp., Summit, NJ), the endectocide Ivermectin (Norbrook Laboratories, LTD., Down, Northern Ireland, UK), the clostidrial vaccine Vision 7 with SPUR (Ivesco LLC., Iowa Falls, IA), and the leptospirosis vaccine Leptoferm-5 (Pfizer, Inc., New York, NY). We then reversed the effects of xylazine HCl with 0.125 mg/kg yohimbine HCl (Kreeger 1996) or 4.0 mg/kg tolazoline HCl (Miller et al. 2004).

We measured previous year cumulative lactation demand as the number of days (up to 84 days representing the approximate time of weaning; DeYoung and Miller 2011) a mother reared a fawn in the previous year. We then added the number of days a mother reared each fawn in a litter in the previous year to calculate the cumulative lactation demand for her. For example, a mother who birthed a twin litter in which one fawn was

reared for 30 days and the other for 50 days would be assigned a previous year cumulative lactation demand value of 80.

We systematically searched each pen within the MSU Deer Unit daily for fawns during 1 June – 2 October, of 2007–2010. We uniquely marked fawns with medium plastic ear tags (Allflex, Dallas, Texas, USA), measured body mass (nearest 0.01 kg) using a digital vertical hanging scale (Pelouze, Bridgeview, Illinois, USA) and collected hair or ear notch samples for DNA collection. DNA Solutions (Oklahoma City, Oklahoma, USA) assigned parentage using DNA based on a proprietary, non-statistical custom structured query language database known as the DNA Solutions Animal Solutions Manager (DASM©). In the pairwise allele comparison DNA Solutions assigned parentage when they excluded all but one sire and one dam based upon a shared allele from each parent at all loci tested (B. G. Cassidy, DNA Solutions, personal communication).

We chemically immobilized and processed juvenile deer 5.5-months after their average birth date during 2007–2011. We repeated the same morphometric measurements and administered the same size-appropriate prophylactics as the adult females and then marked individuals with a large plastic tag (Allflex, Dallas, TX) in each ear. We then transported an equal sample of juvenile males to each satellite facility.

We chemically immobilized adult males (≥ one-year-old) for data collection during October–November, 2008–2013. We measured body mass to the nearest 0.01 kg, administered the same size-appropriate prophylactics as the adult females and measured the inside spread, basal circumference and beam length of antlers prior to their removal. We removed antlers about 3 cm above the burr with a reciprocating saw or diamond wire

but did not remove antlers less than 3 cm long. We calculated an antler score similar to the gross non-typical Boone and Crockett score (Nesbitt et al. 2009), but measured less than 4 circumferences when antlers contained less than 3 tines. For example, a main beam with 2 tines only included 3 circumference measurements. The Mississippi State University Institutional Animal Care and Use Committee approved all capture, handling, and marking techniques under protocols 04–068, 07–036, 10–033 and 13–034.

3.2.3 Data analyses

We developed the same candidate set of four models (DM, DEL, DMEL and IMEL) separately for yearling, two- and three-year-old males. This allowed us to assess whether maternal and/or early life characteristics consistently influenced male body mass and antler size throughout maturity. However, not every male survived to three-years of age; therefore, we only included males that had survived to a given age for each analysis.

Several of our variables may be interpreted as maternal and/or early life characteristics. We categorized birth date as a stand-alone early life characteristic; juvenile growth ceases during winter months as a fawn's metabolism shifts from a positive to negative energy balance (Verme and Ullrey 1984). Birth date thus dictates the number of growing days an individual has until cessation of growth, which can ultimately influence survival (Feder et al. 2008). Weaning mass, and presumptively juvenile mass, is also an important characteristic; it encompasses maternal care, is related to body mass later in life and also influences survival (Festa-Bianchet et al. 2000, Feder et al. 2008, Therrien et al. 2008). Therefore, we included juvenile body mass in both maternal and early life models. Additionally, twin litters comprised about 78% of all litters in our

sample, so we used only twins in our analysis to remove variation related to the uneven distribution of litters.

Path analysis is a general form of multiple regression and is used to test theoretical relationships where multiple variables are correlated (Mitchell 2001, Schumacker and Lomax 2004). However, due to the hierarchical structure of our data (repeated measurements of mothers across years) we tested our path models using Shipley's d-sep (directional separation) procedure to test the hypotheses of conditional independence (Shipley 2000*a*, Shipley 2009). For example, to test the conditional independence hypothesis of X and Y given variables Z_1 and Z_2, we obtained the null probability (p-value associated with the appropriate variable) that the slope of X was zero in a linear mixed model whose fixed structure is $Y \sim Z_1 + Z_2 + X$ (Thomas et al. 2007). If our cause-effect paths among variables in our hypotheses (Figure 3.1) are correct, the pattern of dependencies and (partial) independencies as shown by the path models are captured by the k mutually independent elements of Shipley's (Shipley 2000*a*, 2003, 2009) d-separation basis set of (partial) independencies. The C statistic, calculated as $C = -2\Sigma\ln(p_i)$ using the k null probabilities (p_i) that are associated with the basis set, follows a $\chi 2$ distribution with $2k$ degrees of freedom (Thomas et al. 2007). However, more than one model may achieve the same level of fit, so we calculated Akaike's Information Criterion corrected for small sample size (AIC_c) according to Shipley (2013) and considered models within 2 ΔAIC_c as competing models (Burnham and Anderson 1998). We used the Bentler Comparative Fit Index (CFI) as an indication of model performance where values range from 0 (no fit) to 1 (perfect fit) with values ≥ 0.90 indicating good fit (Palomares et al. 1998, Shipley 2000*b*, Schumacker and Lomax 2004). We then fit mixed

models with the restricted maximum likelihood using the lmer function in the lmer4 package in Program R (R Development Core Team 2008 version 3.1.3; Bates et al. 2014). The magnitude of a path coefficient (calculated as a standardized regression coefficient) indicates the degree of influence a variable has on another variable (Palomares et al. 1998). We used the same mixed model structure as described for the d-sep analysis to calculate path coefficients. We accounted for multiple measurements of individual mothers as well as regional variation in adult body mass (Strickland and Demarais 2000) by including maternal ID and source soil region as random effects when running mixed models for the d-sep analysis. We normalized body mass by natural log transformation and determined that relationships among variables were linear.

3.3 Results

Some average characteristics of mothers used in each analysis varied due to a reduction in sample size within older male age groups (Table 3.1). Previous-year cumulative lactation demand of mothers varied from 63 days for the two-year-old male age group to 83 days for the yearling male age group. However, age at conception and body mass of mothers were consistent within each male age group (Table 3.1).

Some average characteristics of males within age groups also varied due to the reduction in sample size within older male age groups (Table 3.2). Body mass and antler score increased at least 63% between one and three-years of age, but birth and juvenile body mass and birth date were consistent within each male age group.

Multiple models achieved good fit (range $P = 0.091–0.953$); however, there was variation at each age group (Table 3.3). Only the DEL and the DMEL models achieved

good fit at all ages. The DM model achieved good fit for yearlings only, while the IMEL model did not fit at any age group.

The DEL model, which included the direct effect of birth date on body mass and antler size, was the best model for each age group (Figure 3.1B; Table 3.4). This model displayed high model weight (w_i = 1.00) and all other models exceeded 50 ΔAIC (Table 3.4). We report independence claims and null probabilities summaries for the DEL model in Appendix 1.

The DEL model consistently depicted direct paths from birth date and juvenile body mass to adult body mass and antler size for each age group. Birth date positively influenced adult body mass at each age group and was strongest for three-year-olds (β = 0.496, *95% CI* 0.184–0.807; Figures 3.2–3.4). Juvenile body mass also positively influenced adult body mass at each age group and displayed the strongest effect for yearlings (β = 0.806, *95% CI* = 0.593–1.018) and two-year-olds (β = 0.712, *95% CI* = 0.425–0.998; Figures 3.2–3.4). Although we reported a direct path from birth date to antler size at each age group, this relationship must be interpreted with caution because the *95% CI*s overlap 0 (Figures 3.2–3.4).

The positive relationship between birth date and adult body mass is evident when examining growth rates and body masses of fawns born at different times. Plotting standardized body mass by standardized birth date for early-, mid- and late-born fawns depicts a positive relationship for mid- and late-born fawns (Figure 3.5). This positive relationship indicates that fawns born later displayed increased growth rates from one- to three-years of age. Mean percent daily growth rates were also larger for mid- and late-born fawns compared to early-born fawns (Figure 3.6). These increased growth rates

ultimately led to mid- and late-born fawns being heavier later in life than early-born fawns (Figure 3.7).

Three variables consistently influenced juvenile body mass in the DEL model. Birth date displayed the strongest effect and negatively influenced juvenile body mass at each age group (range β = -0.508 – -0.469; Figures 2–4). Previous year cumulative lactation demand also negatively influenced juvenile body mass at each age group (range β = -0.368 – -0.254; Figures 3.2–3.4). Birth mass positively influenced juvenile body mass for yearlings (β = 0.318, *95% CI* = 0.059–0.577) and two-year-olds (β = 0.319, *95% CI* = 0.025–0.613) but not for three-year-olds (Figures 3.2–3.4). Although we reported direct paths from maternal age and maternal body mass to juvenile body mass, these relationships must be interpreted with caution as the *95% CIs* overlap 0 for each age group.

Maternal characteristics displayed consistent effects at each age group for the DEL model. Maternal age positively influenced maternal body mass (range β = 0.600 – 0.648) and previous year cumulative lactation demand (range β = 0.584 – 0.641) at each age group (Figures 3.2–3.4). Previous year cumulative lactation demand, in turn, positively influenced birth mass at each age group (range β = 0.241 – 0.340; Figures 3.2–3.4). Maternal body mass also positively influenced birth mass at each age group (range β = 0.513 – 0.625; Figures 3.2–3.4).

3.4 Discussion

Our results support the DEL model, which depicts the persistent positive influence of birth date on adult body mass through three-years of age for captive male white-tailed deer. The positive effect of birth date on body mass increased as males aged,

indicating that late-born individuals over-compensated for a late start to life. Compensatory growth of body mass in relation to late birth has been reported for the moor frog *(Rana arvalis*; Orizaola et al. 2010) and king penguins (*Aptenoytes patagonicus*; Stier et al. 2014) though it has not been found in large mammals such as bison (*Bison bison*; Green and Rothstein 1993) and moose (*Alces alces*; Solberg et al. 2008). This may indicate that free-ranging large mammals do not have access to high-quality resources needed to display maximum growth rates required for compensatory or over-compensatory growth. This result also identifies body mass as an important secondary sexual characteristic because compensatory growth likely incurs detrimental effects later in life (Dmitriew 2011).

Compensation of body mass must positively influence reproductive success because there are consequences to displaying increased growth rates (Arendt 1997, Dmitriew 2011). Body mass positively influences reproductive success for many ungulate species (bighorn sheep, Coltman et al. 2001; red deer, Clutton-Brock et al. 1982, North American elk, *Cevrus canadensis*, Kie et al. 2013). Late birth may negatively influence an individual's reproductive success if that individual is lighter later in life (Mangel and Munch 2005). Compensation of body mass allows late-born individuals that are lighter earlier in life to become more competitive in gaining access to mates later in life. Improved reproductive success may therefore offset any negative consequences of displaying compensatory growth.

Over-compensation may have a greater positive influence on reproductive success than compensation alone. Males that over-compensate are heavier at a given age than males that compensate only. Although over-compensation likely incurs the same

consequences as compensation, over-compensation may be more advantageous than compensation alone if those males experience greater reproductive success from being heavier. If so, shorter life as a result of over-compensation (Arendt 1997, Dmitriew 2011) may be beneficial if an individual is more reproductively successful during their life-span than if they had not over-compensated. Selection may therefore favor individuals that over-compensate for a late start to life as growth rates are heritable (Blouin 1992, Silverstein et al. 2009).

Although we report that male white-tailed deer over-compensate for a late start to life, we were unable to identify a specific mechanism(s) that facilitated over-compensation; though, there are several possibilities. Hyperphagia is the most common mechanism used to explain compensatory growth in food restriction studies (Ali et al. 2003). However, hyperphagia alone may not fully explain the over-compensation of late-born offspring in our study. Individuals are more likely to over-compensate if, in addition to hyperphagia, they also display the ability to differentially allocate nutrients to growth of certain tissues (skeletal, muscle, etc.; Gurney et al. 2003) and/or grow more efficiently (Skalski et al. 2005). This would be essential for concentrate selectors such as white-tailed deer, as rumen size limits food consumption (Hewitt 2011).

Photoperiod may also facilitate over-compensation. Photoperiod influences growth rates in alpine beetles (*Oreina elongate*; Margraf et al. 2003), temperate butterflies (*Pararge aegeria*; Gotthard 2000) and alpine caddisflies (*Allogamus uncatus*; Shama and Robinson 2006). Though the influence of photoperiod on growth rates in ungulates has not been documented, it does greatly affect other life-history traits such as timing of reproduction (Demarais et al. 2000) and antler growth (Demarais and

Strickland 2011). Therefore, in regions where there is large variation in birth dates, photoperiod may influence growth rates of late-born offspring as day length differs during gestation and lactation for mothers of late-born offspring.

The negative influence of previous year cumulative lactation demand on juvenile body mass suggests that mothers are unable to consistently rear heavy offspring. Lactation is the most energetically demanding time period for a mother and often requires mobilization of body reserves, which decreases maternal body condition (reviewed in Parker et al. 2009, Monteith et al. 2013, Simard et al. 2014). Maternal body condition, in turn, positively influences reproductive success in a given year (reviewed in Parker et al. 2009). Mothers in our study had adequate nutrition available (high-quality diet fed *ad libitum*) to replenish their body condition after successfully reproducing. Therefore, successfully rearing offspring in a previous year negatively influences a mother's ability to rear heavy offspring in a current year, regardless of the quality of nutrition available (Green and Rothstein 1991, Feder et al. 2008).

The influences of birth mass and birth date on juvenile body mass indicate that white-tailed deer fawns displayed a silver spoon effect. Silver spoon effects describe situations where individuals are born under favorable conditions which positively influences their phenotype and persists throughout life (Grafen 1988). Being an early-born, heavy fawn was advantageous as birth mass positively influenced juvenile body mass while birth date negatively influenced juvenile body mass. Our results support other studies of long-lived mammals (roe deer, *Capreolus capreolus*, Gaillard et al. 1993, mountain goats, *Oreamnos americanus*, Côté and Festa-Bianchet 2001; moose, Saether et al. 2003; bighorn sheep, Feder et al. 2008). Silver spoon effects may therefore indirectly

influence adult phenotype as juvenile body mass positively influenced adult body mass and antler size. However, our results also suggest that juveniles were unable to compensate for a poor start to life, which contradicts the over-compensation we report for adults.

Growth cessation related to photoperiod likely influences a juvenile's ability to display compensatory growth. Photoperiod influences energy intake and utilization in white-tailed deer fawns as energy intake increases and utilization becomes more efficient, ultimately leading to increased fat deposition and body mass gain regardless of diet quality, as days became shorter (Verme and Ozoga 1980, Abbott et al. 1984). White-tailed deer fawns also voluntarily reduce food intake and cease growth during winter months (Thompson et al. 1973). Therefore, late-born fawns simply may not have had enough time to compensate before the cessation of growth.

The differing effects of birth date on juvenile and adult body mass may reflect different life-history strategies of male white-tailed deer. Winter severity increases with increasing latitude across the whitetails range. Increased body mass thus increases probability of over-winter survival for ungulates that experience severe winters (Côté and Festa-Bianchet 2001, Loison et al. 1999). At latitudes where winter severity influences survival, early birth is advantageous as early-born offspring are heavier at weaning compared to late-born offspring (Feder et al. 2008). Conversely, where winters are mild and do not impede survival, there is less selective pressure associated with early birth, as displayed by the range of birth dates in our study. If birth date does not influence survival at southern latitudes, then males are able to reach an age where over-compensation occurs. Future studies occurring at northern latitudes should assess whether birth date

displays persistent effects on male body mass through maturity; this would allow for further knowledge of the variation of white-tailed deer life-history strategies.

We also found consistent relationships among maternal characteristics. Maternal age did not influence birth nor juvenile body mass in our study; however, it is generally described as an important characteristic that is associated with offspring body mass for ungulates, and is often used as a surrogate for other maternal characteristics such as body mass and condition (Verme 1989, Solberg et al. 2007, Loison et al. 2004). Maternal body mass did, however, positively influence birth mass, which is consistent with previous research (Favre et al. 2008, Steiger 2013, Michel et al. 2015). This relationship emphasizes the importance of including both maternal age and maternal body mass in studies assessing the relationship between maternal and offspring characteristics.

We also observed a weak but positive relationship between previous year cumulative lactation demand and fawn birth mass, suggesting that mothers that reared offspring to weaning in the previous year birthed heavier offspring in the current year. This contradicts Feder et al. (2008) who reported that mothers that successfully reared offspring in the previous year produced lighter offspring in the current year. However, this contradiction may indicate differences in diet quality between studies, as low quality mothers who experience nutritional restrictions may not be able to produce high-quality offspring in consecutive years (Hamel et al. 2009).

3.5 Conclusion

Male white-tailed deer display alternate strategies to increase body mass throughout their life. Over-compensation identifies body mass as an important secondary sexual characteristic related to fitness as compensatory growth likely accrues negative

costs. However, white-tailed deer fawns also display a silver spoon effect as early-born, heavy fawns are also heavy juveniles. Heavy juveniles are also larger, later in life. Silver spoon effects may therefore indirectly influence adult phenotype through its influence on juvenile body mass. We hypothesize that male white-tailed deer display alternative strategies that potentially influence reproductive success; males are either born with a silver spoon, which potentially allows them to be heavy later in life or they over-compensate for late-birth if the environment allows.

Table 3.1 Mean characteristics of mothers held at the MSU Deer Unit in Oktibbeha County, Mississippi, USA, 2005–2010 that produced males used in each respective male age group analysis. Mean ± SD, (range).

Male Age Group	Number of Mothers	Previous Year Cumulative Lactation Demand (days)	Age at Conception (years)	Maternal Body Mass at Conception (kg)
Yearlings	33	82.8 ± 70.2	2.1 (1-4)	45.5 ± 6.5
Two-Year-Olds	29	62.8 ± 70.6	1.8 (1-4)	44.2 ± 7.3
Three-Year-Olds	27	73.2 ± 73.4	2.03 (1-4)	45.3 ± 7.3

Table 3.2 Mean characteristics of male white-tailed deer used in each age group at captive research facilities in Noxubee, Attala, Copiah, and Scott Counties, Mississippi, USA, 2007–2013. Mean ± SD, (range).

Male Age Group	*n*	Birth Date	Body Mass (kg)			Antler Score (cm)
			Fawn	Juvenile	At Age	
Yearlings	48	July 26 (June 21 - September 22)	2.6 ± 0.5	29.6 ± 5.3	53.7 ± 9.4	103.1 ± 52.3
Two-Year-Olds	42	July 27 (June 21 - September 22)	2.6 ± 0.4	29.1 ± 5.1	72.9 ± 11.8	230.9 ± 38.2
Three-Year-Olds	37	July 27 (June 21 - September 22)	2.6 ± 0.5	29.4 ± 5.2	88.2 ± 13.9	293.1 ± 40.8

Table 3.3 Models that fit data from male white-tailed deer held at captive research facilities in Noxubee, Attala, Copiah, and Scott Counties, Mississippi, USA, 2007–2013.

Model	*C*	*DF*	*P*	*n*
Yearlings				
DEL	18.642	18	0.414	48
DM	12.610	10	0.246	48
DMEL	1.584	6	0.953	48
Two-Year-Olds				
DEL	26.371	18	0.091	42
DMEL	9.477	6	0.148	42
Three-Year-Olds				
DEL	26.158	18	0.096	37
DMEL	7.050	6	0.316	37

C values follow a X^2 distribution, thus p-values ≥ 0.05 indicates a model did not differ from our data and were used for further analysis.
DM: Direct Maternal Characteristics Model
DEL: Direct Early Life Characteristics Model
DMEL: Direct Maternal and Early Life Characteristics Model

Table 3.4 Selection results for fitted models describing the influence of maternal and early life characteristics on body mass and antler size in the yearling-, two-, and three-year age groups using AICc for male white-tailed deer at captive research facilities in Noxubee, Attala, Copiah, and Scott Counties, Mississippi, USA, 2007–2013.

Model	*K*	*ΔAICc*	w_i	*CFI*
Yearlings				
DEL	27	0.00	1.00	0.93
DM	31	50.37	0.00	0.95
DMEL	33	79.63	0.00	0.99
Two-Year-Olds				
DEL	27	0.00	1.00	0.87
DMEL	33	167.61	0.00	0.95
Three-Year-Olds				
DEL	27	0.00	1.00	0.86
DMEL	33	572.89	0.00	0.96

K indicates the number of parameters and wi indicates the AICc weight. Bentler Comparative Fit Index (CFI) indicates the performance of proposed models. Our top model is represented in Figures 3.2–3.4.
DM: Direct Maternal Characteristics Model
DEL: Direct Early Life Characteristics Model
DMEL: Direct Maternal and Early Life Characteristics Model

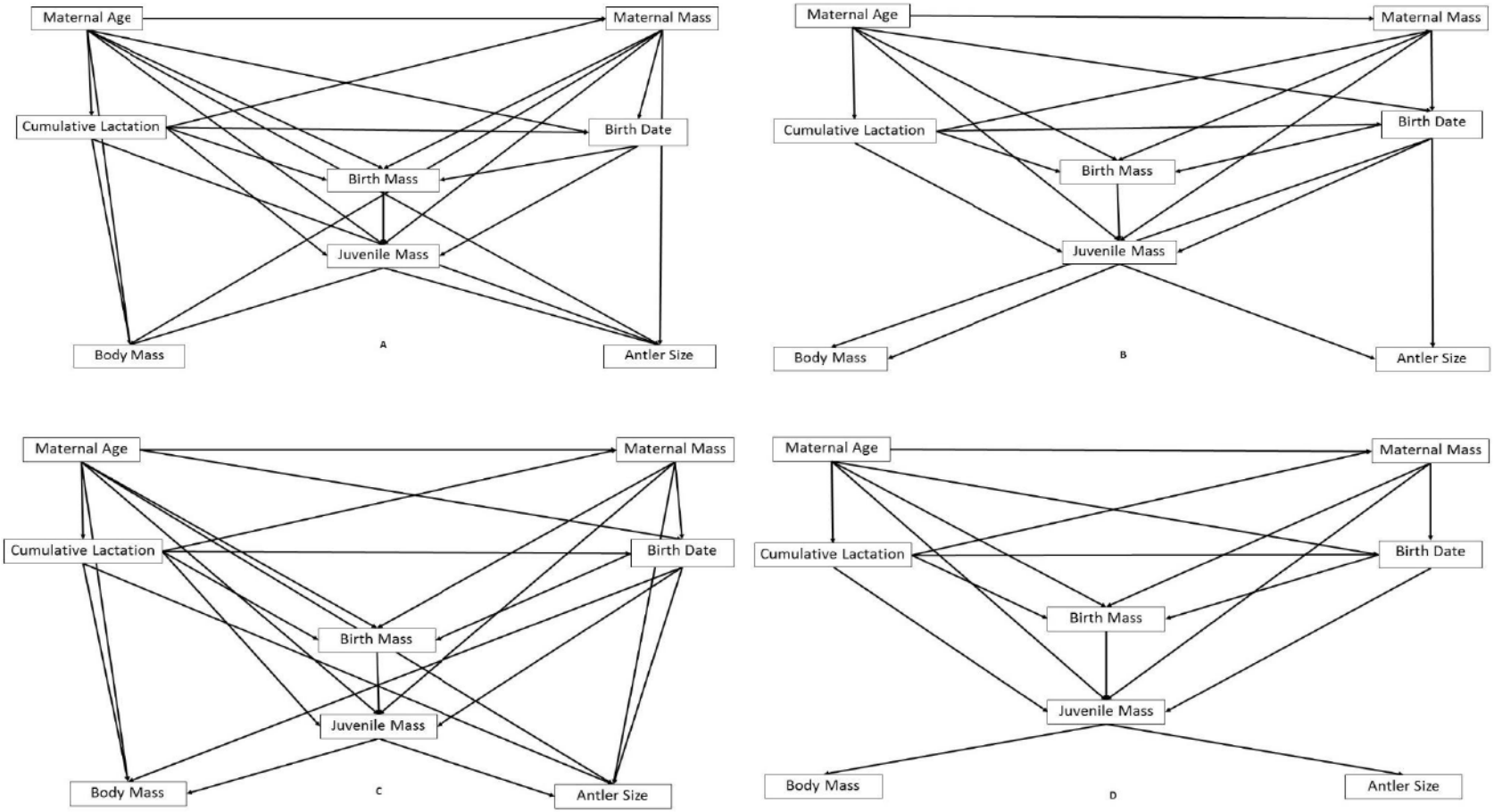

Figure 3.1 Conceptual models depicting different hypotheses about the influence of maternal and early life characteristics of male white-tailed deer housed at captive research facilities in Noxubee, Attala, Copiah, and Scott Counties, Mississippi, USA, 2007–2013.

A. Direct Maternal Characteristics Model. B. Direct Early Life Characteristics Model. C. Direct Maternal and Early Life Characteristics Model. D. Indirect Maternal and Early Life Characteristics Model.

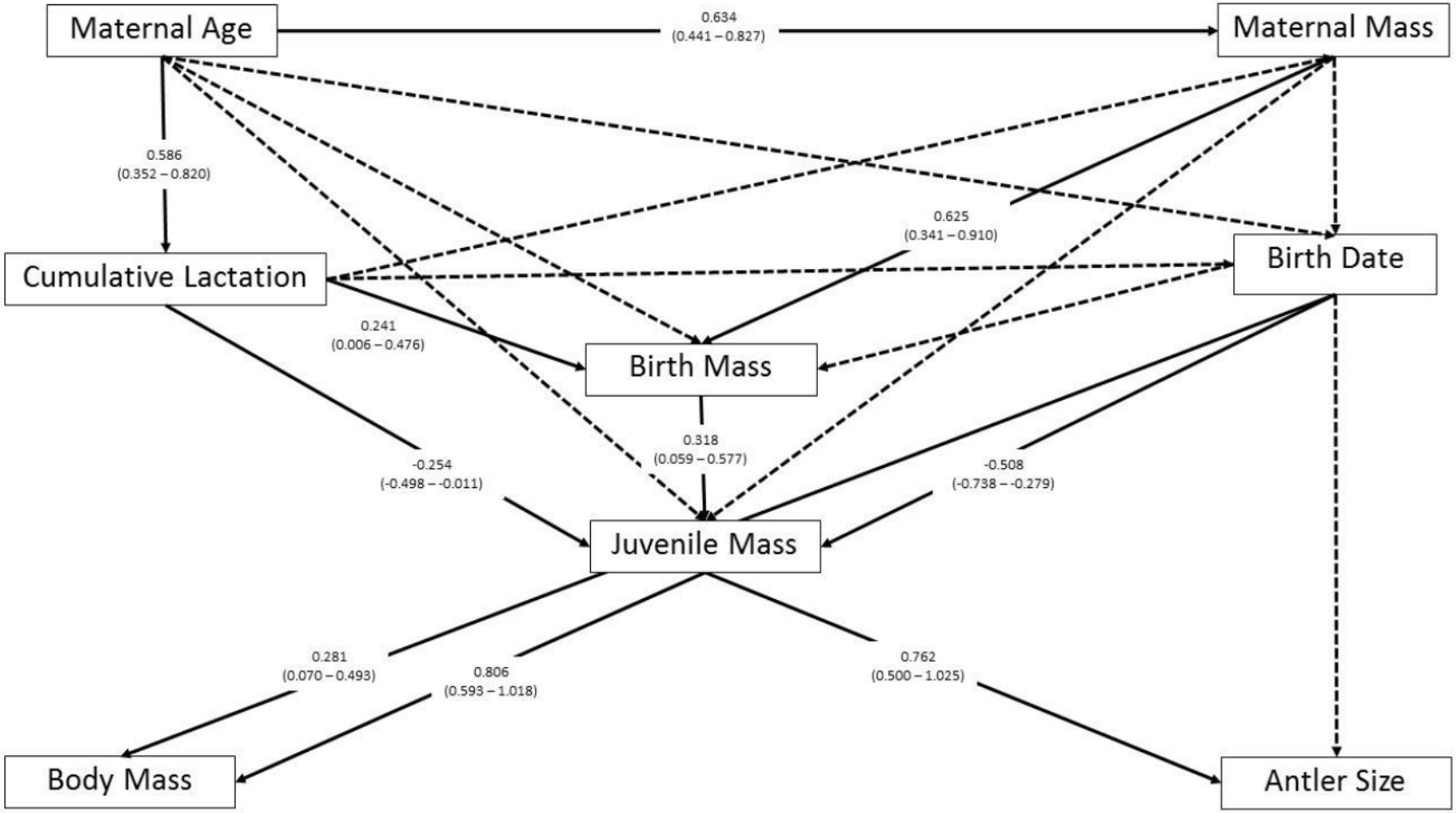

Figure 3.2 The Direct Early Life characteristics model was our top model and depicts the direct effect of birth date on body mass for yearling male white-tailed deer housed at captive research facilities in Noxubee, Attala, Copiah, and Scott Counties, Mississippi, USA, 2007–2013.

95% CI listed below the standardized regression coefficients. Dashed lines indicate 95% CI overlapped 0.

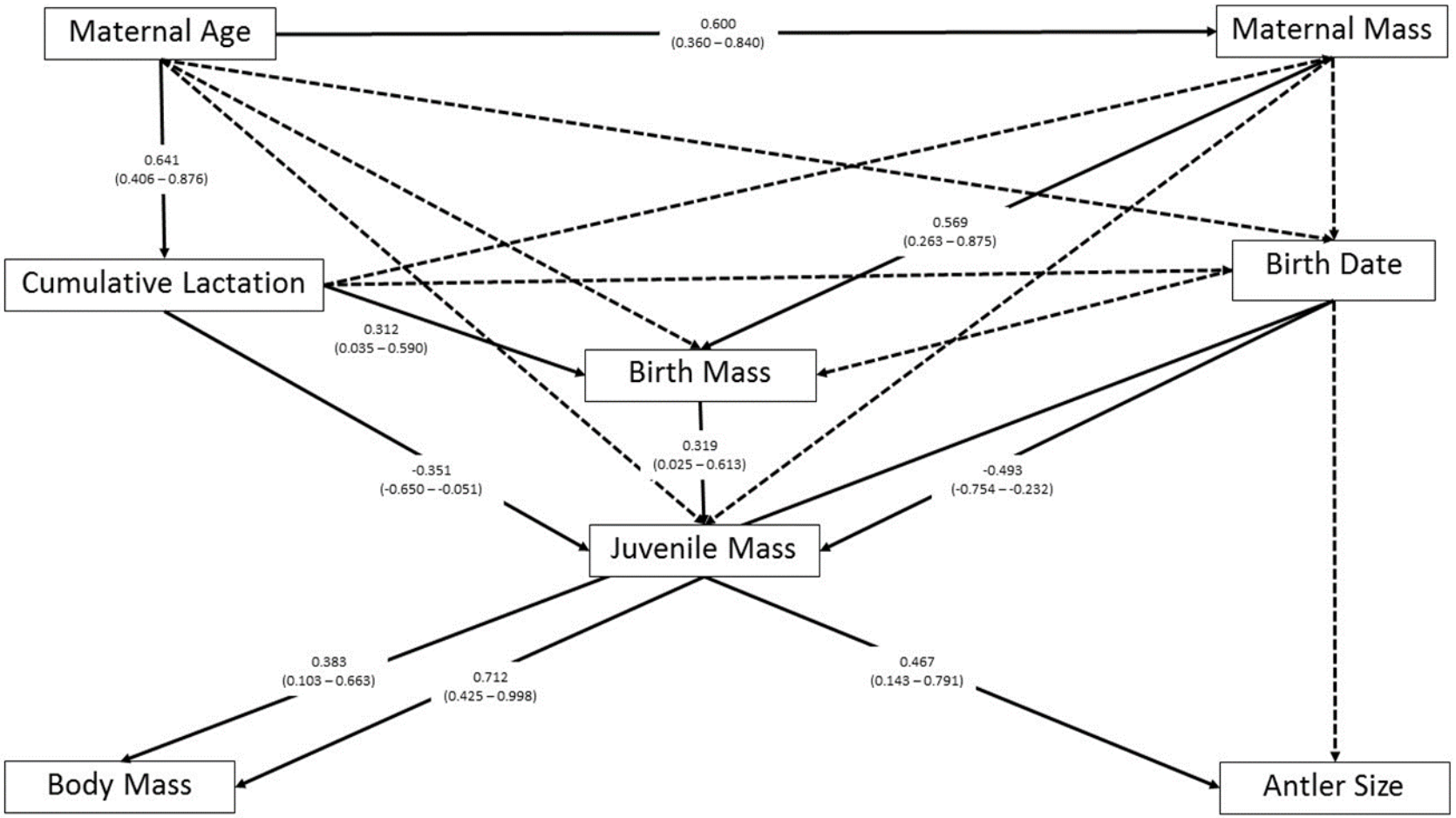

Figure 3.3 The Direct Early Life characteristics model was our top model and depicts the direct effect of birth date on body mass at two-years of age for male white-tailed deer housed at captive research facilities in Noxubee, Attala, Copiah, and Scott Counties, Mississippi, USA, 2007–2013.

95% CI listed below the standardized regression coefficients. Dashed lines indicate *95% CI* overlapped 0.

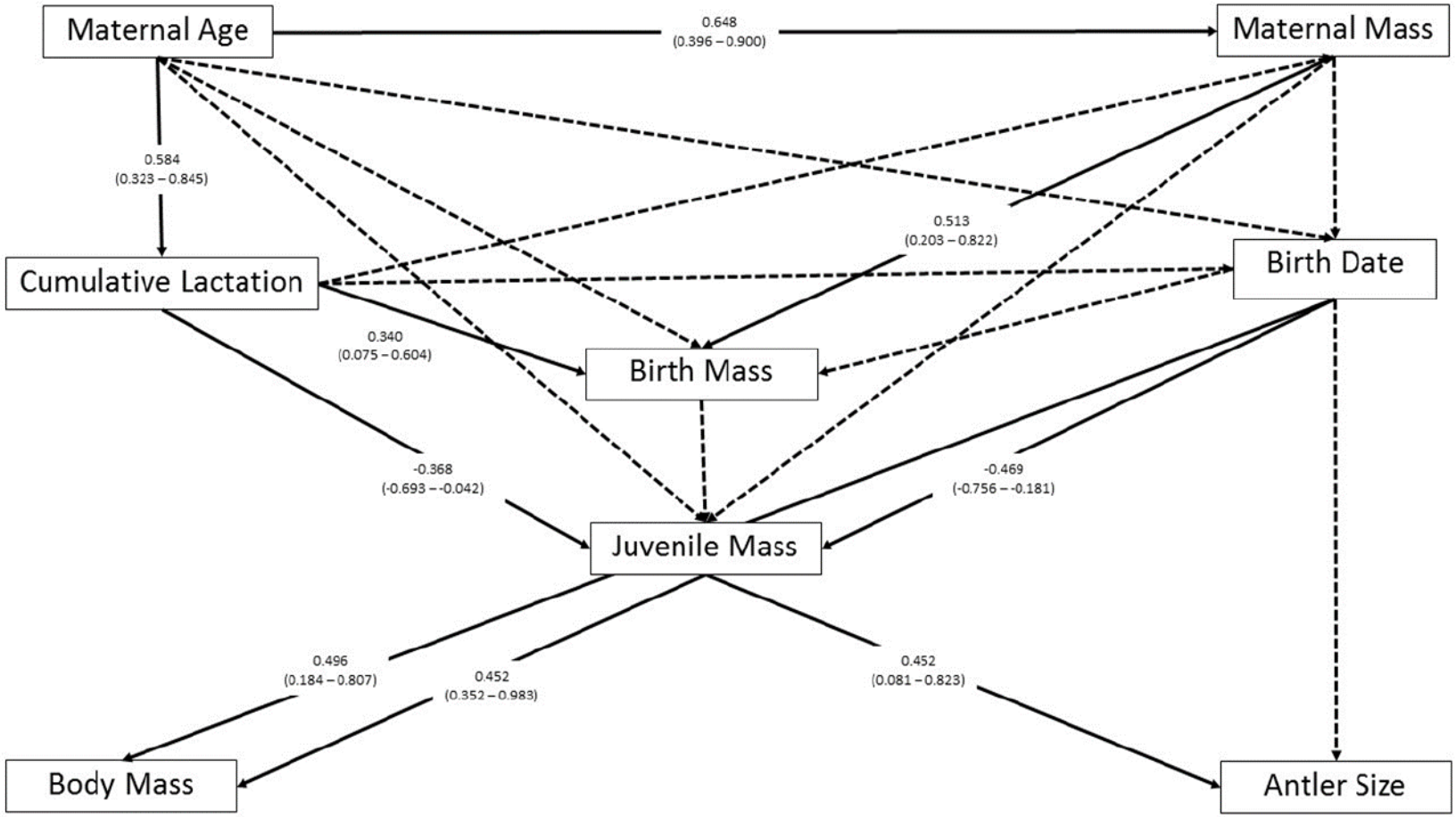

Figure 3.4 The Direct Early Life Characteristics model was our top model and depicts the direct effect of birth date on body mass at three-years of age for male white-tailed deer housed at captive research facilities in Noxubee, Attala, Copiah, and Scott Counties, Mississippi, USA, 2007–2013.

95% CI listed below the standardized regression coefficients. Dashed lines indicate *95% CI* overlapped 0.

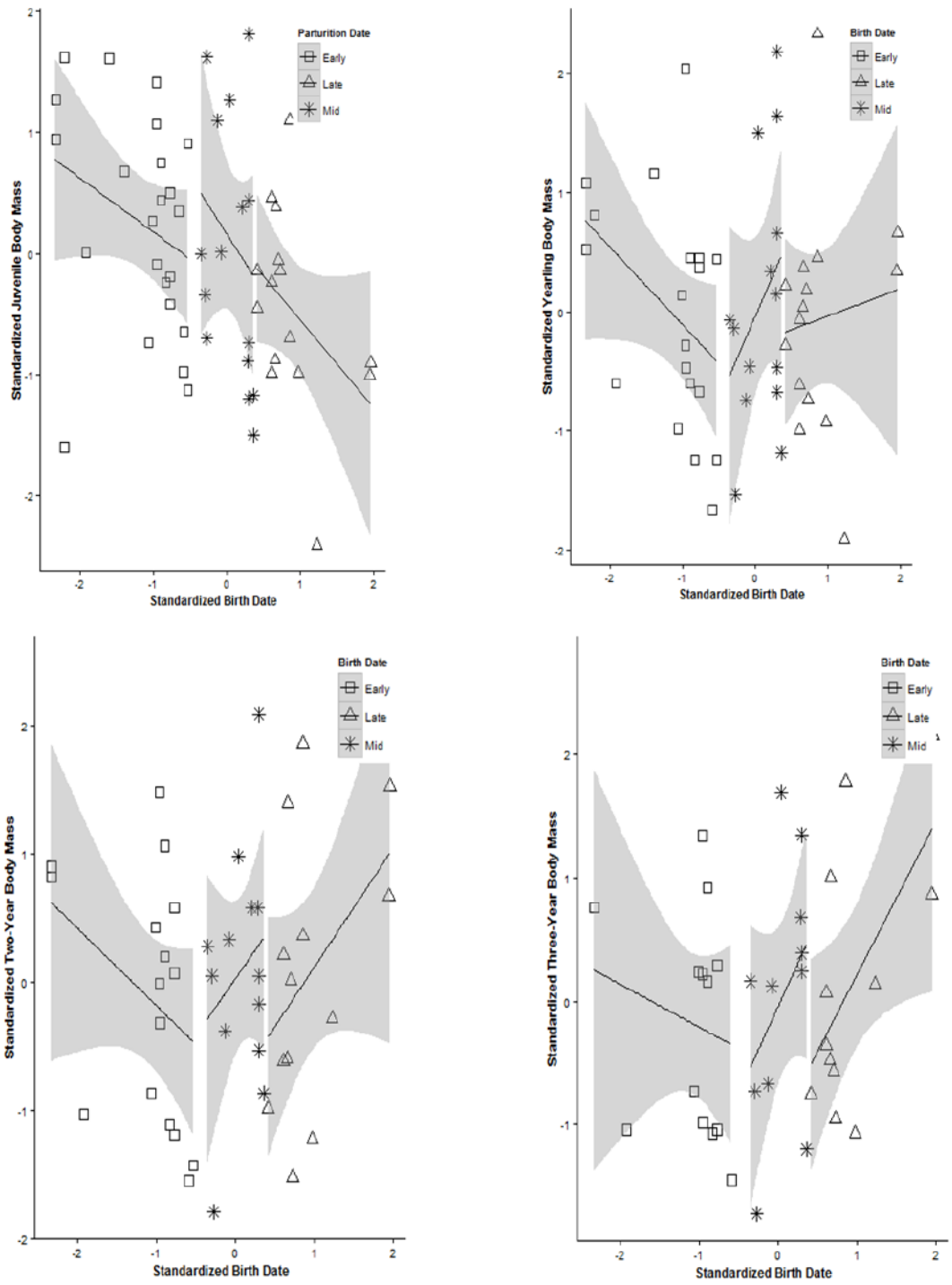

Figure 3.5 Relationships between birth date and body mass of early-, mid- and late-born juvenile, yearling, two- and three-year old male white-tailed deer.

Birth date and body mass were standardized by soil source region. Positive slope for mid- and late-born fawns as yearlings, two- and three-year-olds indicates increased growth rates. Shaded areas indicate associated SEs.

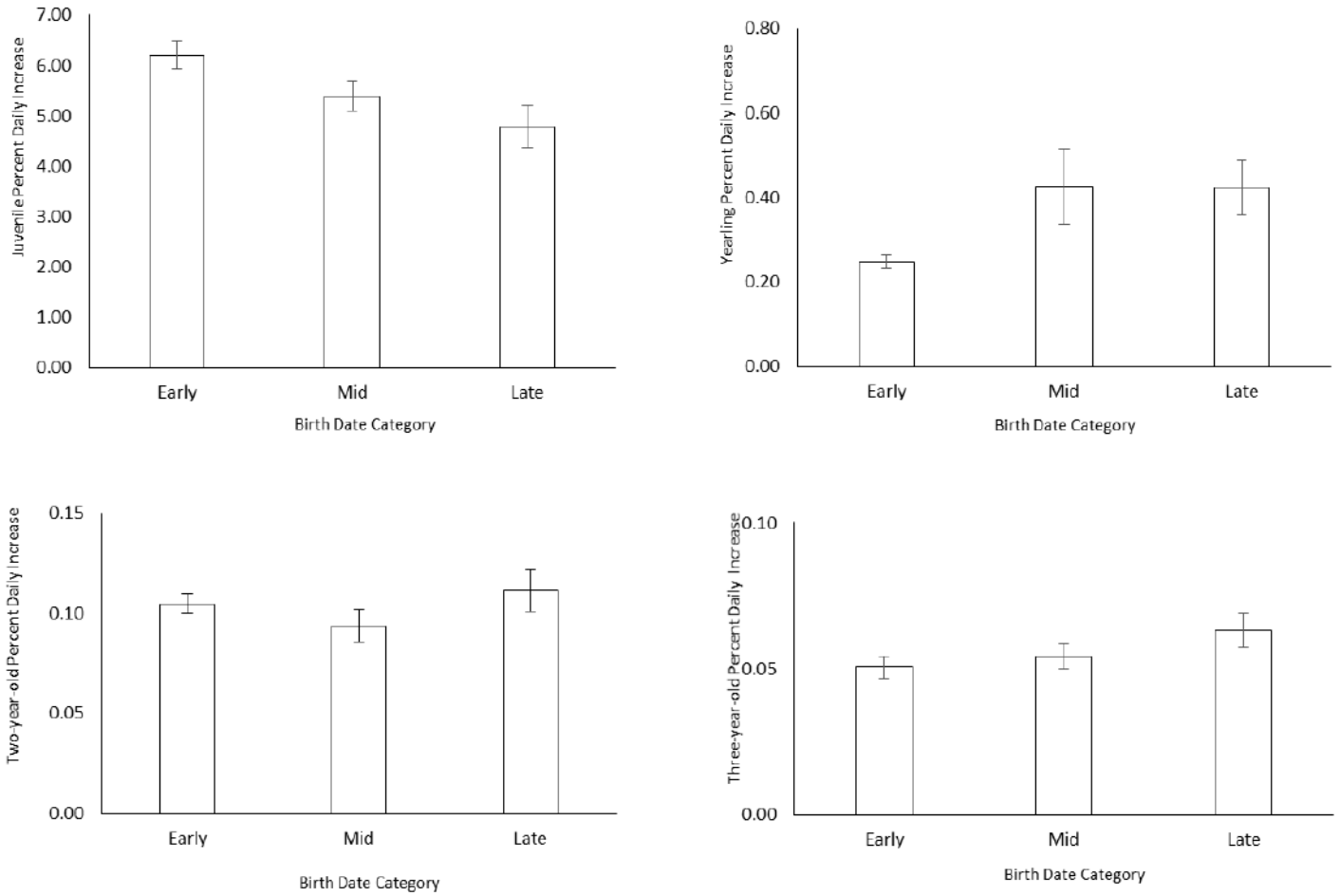

Figure 3.6 Mean age specific growth rates for early-, mid- and late-born juvenile, yearling, two- and three-year old male white-tailed deer.

Birth date was standardized by soil source region. Error bars indicate associated SEs.

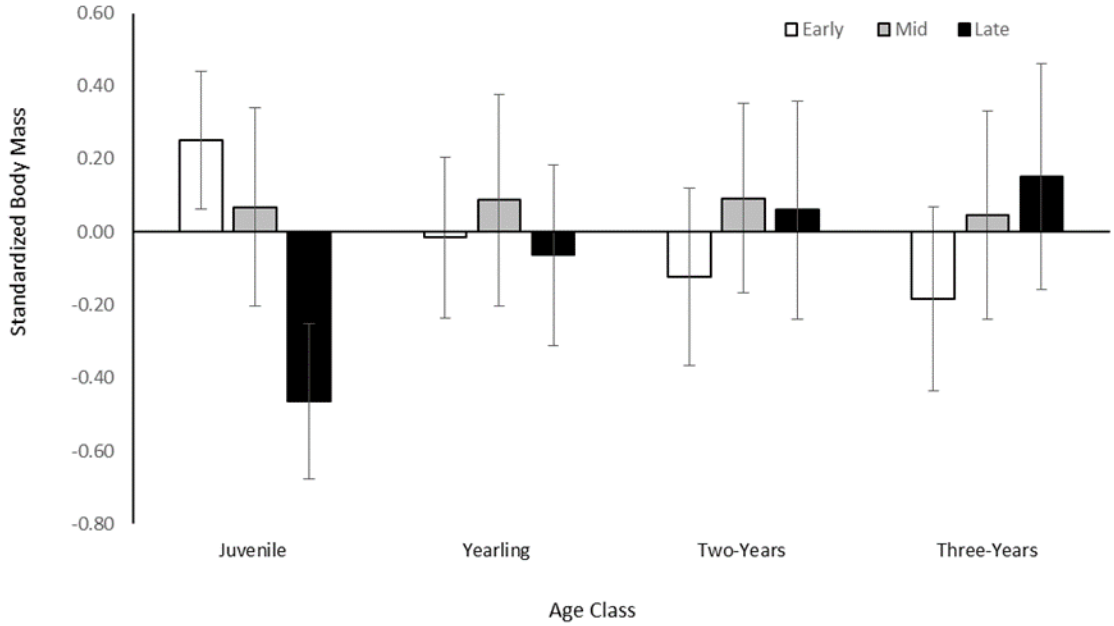

Figure 3.7 Mean age specific body mass for early-, mid- and late-born juvenile, yearling, two- and three-year old male white-tailed deer.

Birth date and body mass was standardized by soil source region. Error bars indicate associated SEs.

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CHAPTER IV

ANTLER CHARACTERISTICS ARE HIGHLY HERITABLE BUT INFLUENCED BY MATERNAL FACTORS

4.1 Introduction

Sport hunting may unintentionally influence the evolutionary trajectory of a population (Allendorf et al. 2008). Possible outcomes of sport hunting include changing the rate of gene flow among neighboring populations, influencing the rate of genetic drift, or decreasing individual fitness (reviewed by Harris et al. 2002). Although there is little empirical evidence of significant genetic changes (reviewed in Mysterud 2011), some change due to harvest is possible as hunter selection within the population is nonrandom (Allendorf et al. 2008). Separate analyses of the same population concluded that trophy hunting reduced horn size in bighorn sheep (*Ovis canadensis*; Coltman et al. 2003, Pigeon et al. 2016). Additionally, Monteith et al. (2013) reported long-term declines in size of harvested antlers and horns for several ungulate species using Boone and Crockett Club records from 1950 to 2008. Therefore, the potential influence of hunting on the genetic structure of game species must be considered.

Though difficult to estimate, heritability is important because it provides a measure of evolvability for a population (Falconer and McKay 1996, Brookfield 2009). As a population metric that describes the degree of resemblance between relatives and is defined as the ratio of additive genotypic variance to phenotypic variance (Falconer and

McKay 1996, Wilson et al. 2010), heritability would affect sensitivity to harvest-related genetic change. Estimating heritability is difficult because non-genetic sources of variation may influence traits of interest. For example, antler characteristics are considered terminal traits because they are fully expressed at maturity and should be highly heritable (Mousseau and Roff 1987, Wilson et al. 2000). However, antler characteristics are also influenced by non-genetic factors, such as habitat quality and land use (Strickland and Demarais 2000, 2008), as well as maternal effects (Mech et al. 1991, Monteith et al. 2009). As such, there is a wide range of heritability estimates reported for white-tailed deer antler characteristics; Lukefahr and Jacobson (1998) reported heritability estimates as low as 0.00 whereas Williams et al. (1994) reported estimates as high as 0.80. The immense importance of white-tailed deer (*Odocoileus virginianus*) as a game species in North America (Adams and Hamilton 2011) justifies the need to clarify heritability estimates for antler characteristics to correctly address the evolvability of populations and to assess efficacy of different, sometimes controversial management strategies (Webb et al. 2012, Demarais et al. *In Press*).

Use of yearling antler size as a criterion for selective harvest management strategies is problematic. Yearlings with larger antlers generally grow larger antlers later in life compared to yearlings that display smaller antlers (Ott et al. 1997, Lewis 2010). However, the expression of yearling antler size may be masked by maternal factors such as parturition date and litter size (Knox et al. 1991, Jacobson 1995, Gray et al. 2002). In contrast, if yearling antler size is efficient in predicting antler size later in life, then using it as a selective harvest criterion could influence genetic structure of a population by increasing the intensity of nonrandom hunter selection (Allendorf et al. 2008). Therefore,

quantifying the degree to which maternal factors affect predictability of future antler size is needed to assess the efficacy of using yearling antler size as a selective harvest criterion.

To better understand heritability of secondary sexual characteristics, we estimated heritability for 6 antler characteristics in male white-tailed deer. Although some studies have reported low heritability (Lukefahr and Jacobson 1998, Kruuk et al. 2002), antler size is positively related to reproductive success (Clutton-Brock et al. 1982, Bartoš and Bahbouh 2006) and is considered a terminal trait (Mousseau and Roff 1987, Bourdon 2000). Therefore, we predict that antler characteristics will be highly heritable.

We quantified the effect of parturition date and litter size on the predictability of future antler size to better understand the effects of maternal factors on expression of genetic potential. Yearling antler size is negatively related to parturition date and litter size and may not display compensation until later in life (Clutton-Brock et al. 1982, Jacobson 1995, Gray et al. 2002). Therefore, we predict that accounting for parturition date and litter size will improve the relationship between 1.5- and 3.5-year-old antler size.

4.2 Study Area

All study animals were born and raised in captivity with similar husbandry practices. Study animals were either born at the Rusty Dawkins Memorial Deer Unit (MSU Deer Unit) or at satellite facilities. The MSU Deer Unit, located in Oktibbeha County, Mississippi, USA, is a 4.9-ha facility subdivided into 5 0.4–0.8 ha pens. Satellite research facilities were located near Macon, Noxubee County; Kosciusko, Attala County; Utica, Copiah County; and Morton, Scott County, Mississippi, USA and consisted of 2 0.7-ha pens. We transported a random sample of approximately 5.5-month old males to

each of 3 satellite facilities across the state. All pens contained water and 2 feeders with 20% crude protein deer pellets (Purina AntlerMax professional High Energy Breeder 59UB, Purina, St. Louis, MO) supplied *ad libitum*. Available forages within pens included various volunteer grasses and forbs along with planted clovers, wheat and oats.

4.3 Methods

We searched pens at the MSU Deer Unit daily for neonate fawns. We uniquely marked fawns with medium plastic ear tags (Allflex, Dallas, TX) and recorded their parturition date.

We sedated deer for sampling at 5.5 months and yearly thereafter through 5.5 years of age. We used a Pneu-Dart projection system (Pneu-Dart, Inc., Williamsport, PA) with a 2:1 mixture of telazol and xylazine HCL with a dosage of 6.6 mg/kg during handling events. We administered yohimbine (0.125 mg/kg; Kreeger 1996) or tolazoline (4.0 mg/kg; Miller et al. 2004) to reverse effects of xylazine. We also administered size-appropriate amounts of the antibiotic Nuflor ™ (Schuering-Plough Animal Health Corp., Summit, NJ), the endectocide Ivermectin (Norbrook Laboratories, LTD., Down, Northern Ireland, UK), the clostidrial vaccine Vision 7 with SPUR (Ivesco LLC, Iowa Falls, IA) and the leptospirosis vaccine Leptoferm-5 (Pfizer, Inc., New York, NY) at each handling event.

DNA Solutions (Oklahoma City, OK) assigned parentage of fawns using DNA from a hair or ear notch sample based on a proprietary, non-statistical custom structured query language database, DASM©. In pairwise allele comparison, DNA Solutions assigned parentage when they excluded all but 1 sire and 1 dam based upon a shared

allele from each parent at all loci tested (B. G. Cassidy, DNA Solutions, personal communication). We assigned litter size from parentage assignments.

We estimated narrow sense heritability (h^2) for antler score, total number of points, main beam length, basal circumference and inside spread for males ≥ 2.5-years of age. We also estimated narrow sense heritability of antler mass for males aged 2.5- through 4.5-years. We calculated an antler score similar to the gross non-typical Boone and Crockett score (Nesbitt et al. 2009), but measured less than 4 circumferences when antlers contained less than 3 tines. For example, a main beam with 2 tines would only include 3 circumference measurements. We measured all tines ≥ 2.5 cm in length. We removed antlers about 3 cm above the burr with a reciprocating saw or diamond wire and weighed antler mass to the nearest 0.1 g for animals aged 1.5- through 4.5-years. Antler sets for 5.5-year-old males were not available for weighing. The Mississippi State University Institutional Animal Care and Use Committee approved all capture, handling, and marking techniques under protocols 07–036, 10–033 and 13–034.

Non-genetic variation must be accounted for when calculating heritability estimates (Bourdon 2000). Soil source region (Strickland and Demarais 2000) and maternal effects (Mech et al. 1991, Monteith et al. 2009) are known to influence antler size. Therefore, we used a mixed model analysis of variance in the lme4 package in Program R (R Development Core Team 2008, version 3.1.3; Bates et al. 2014) to assess the influence of soil source region and generation (a proxy for maternal effects) on each antler characteristic before inclusion in the animal model. We used each antler characteristic as a response variable and soil source region, generation and age as explanatory variables. We included year as a random effect to account for repeated

measurements of individuals. We only included soil source region and generation in the animal model if they were significant in the mixed model analysis of variance ($P \leq 0.05$; Table 4.1). We included age as a fixed effect in the animal model to account for its known influence on antler size (Strickland and Demarais 2000).

We used an animal model within the Monte Carlo Markov Chain generalized linear mixed model (MCMCglmm) framework in the MCMCglmm package in Program R (R Development Core Team 2008, version 3.1.3; Hadfield 2010) to calculate heritability. For each model, we used uninformative priors and ran 100,000 iterations for each of 2 chains. We sampled every 10th iteration after a 50,000-iteration burn-in period. We examined trace plots for convergence of each variable as well as for convergence between chains. We confirmed there were no autocorrelations between iterations within each model. We included individual as a random effect to account for repeated measurements. Small sample size precluded us from assessing heritability at each age (i.e., for yearlings, 2.5-year-olds, 3.5-year-olds, etc.); therefore we pooled data from 2.5- to 5.5-year-olds for analysis. Yearlings have only reached about 28% of their maximum antler size whereas 2.5-year-olds have reached about 62% of their maximum antler size (Demarais and Strickland 2011). Therefore, we did not include yearlings in our analysis because we grouped ages. We used the same model structure for the heritability analysis and mixed model analysis of variance.

We used a generalized linear mixed model in the lme4 package to assess whether 1.5-year-old antler size was a good predictor of antler size later in life. We used 1.5-year antler size to predict 2.5- and 3.5-year antler size. We also used 2.5-year antler size to predict 3.5-year antler size. We converted parturition date to Julian date and included it

and litter size as random effects. We calculated Marginal (fixed effects only) and Conditional (fixed and random effects) R^2 values according to Nakagawa and Schielzeth (2013) to assess whether maternal factors influenced predictability.

4.4 Results

We sampled 37 sires and 92 dams that produced 97 unique male offspring. Mean parturition date was July 28 (range June 9–October 2) and mean litter size was 1.9 (range 1–3) for the 50 males with known birth dates that were included in the predictability analyses. Antler size was >300% greater at 5.5-years than at 1.5-years of age (Table 4.2).

All antler characteristics were highly heritable (Table 4.3). Antler score displayed the highest heritability ($h^2 = 0.84$, *95% CI* = 0.77–0.89, $n = 218$) whereas total number of points displayed the lowest ($h^2 = 0.63$, *95% CI* = 0.49–0.74, $n = 218$).

Accounting for the maternal factors of birth date and litter size improved predictive relationships among all ages. Yearling antler size was a moderate predictor of 2.5-year (Marginal $R^2 = 0.45$, $P < 0.001$, $n = 50$) and 3.5-year antler size (Marginal $R^2 = 0.38$, $P < 0.001$, $n = 50$). Accounting for parturition date and litter size improved the relationship between 1.5- and 2.5-year antler size by nearly 90% (Conditional $R^2 = 0.85$) and between 1.5- and 3.5-year antler size by nearly 95% (Conditional $R^2 = 0.74$). Antler size at 2.5-years was a strong predictor of 3.5-year antler size (Marginal $R^2 = 0.63$, $P < 0.001$, $n = 50$); accounting for parturition date and litter size improved the relationship only 25% (Conditional $R^2 = 0.79$).

4.5 Discussion

Our finding that secondary sexual characteristics are highly heritable for male white-tailed deer supports our prediction and is consistent across taxa. Our results substantively support studies of ungulates where antler size for red deer (h^2 = 0.85, Van den Berg and Garrick 1997; h^2 = 0.81, Ward et al. 2014) and white-tailed deer (h^2 = 0.80, Williams et al. 1994) as well as horn size for bighorn sheep (h^2 = 0.69, Coltman et al. 2003) were highly heritable. Feather color for birds is also highly heritable (*Ficedula hypoleuca*, h^2 = 0.88, Alatalo et al. 1994; *Tyto alba*, h^2 = 0.81, Roulin and Dijkstra 2003; *Strix aluco*, h^2 = 0.72, Brommer et al. 2005; *Hirundo rustica rustica*, h^2 = 0.81, Saino et al. 2013). Similarly, the number of spots (h^2 = 0.62), spot brightness (h^2 = 0.82) and dorsal fin length (h^2 = 0.78) are highly heritable for guppies (*Poecilia reticulate*; Karino and Haijima 2001). Secondary sexual characteristics should be highly heritable, regardless of the characteristic (coloration, fin length, antlers or horns), because these characteristics positively influence reproduction (Safran and McGraw 2004, Bartoš and Bahbouh 2006, Karino and Urano 2008). Thus, high heritability likely ensures that successful phenotypes will persist in a uniform environment.

Although secondary sexual characteristics are highly heritable, there are inconsistencies in the literature. For example, Hadfield et al. (2006) reported that heritability of feather coloration was weak for a population of blue tits (*Parus caeruleus*; h^2 = 0.11). Kruuk et al. (2002) also reported that red deer antler mass was moderately heritable (h^2 = 0.35) and Wang et al. (1999) reported that red deer antler velvet mass was lowly heritable (h^2 = 0.27). Similarly, the largest heritability estimate reported by

Lukefahr and Jacobson (1998) for white-tailed deer was for antler mass ($h^2 = 0.43$). There are several reasons, however, why heritability estimates may differ among studies.

Heritability is a population metric and therefore differences among populations may influence estimates (Falconer and McKay 1996). Our estimates, as well as those of Williams et al. (1994), were almost double Lukefahr and Jacobson's (1998) estimates; however, these differences may be related to confounding factors associated with Lukefahr and Jacobson's study population. Lukefahr and Jacobson (1998) raised deer in Mississippi but parent source populations were from the states of Mississippi, Michigan, Ohio, Pennsylvania, Virginia, Texas and Wisconsin, USA which fall within the range of 4 recognized subspecies (Heffelfinger 2011). All of our source populations originated within Mississippi, USA. Similarly, all source populations used by Williams et al. (1994) originated from Texas, USA. The inability of Lukefahr and Jacobson (1998) to account for the large regional variation of their source population may have influenced their heritability estimates.

Variation in age structure of study populations may also explain some differences in heritability estimates of white-tailed deer. We grouped males aged 2.5- through 5.5-years for our analysis whereas Lukefahr and Jacobson (1998) grouped males aged 3.5- through 7.5-years. Caution must be used when comparing heritability estimates of antler characteristics derived from different age groupings (i.e., 3.5–7.5-years vs. 2.5–5.5-years) because antlers do not reach their maximum size until 5- or 6-years (Strickland and Demarais 2000). Therefore, relative differences in the amount of expression of antler size displayed when using different age groupings may introduce additional variation into the analysis.

Although secondary sexual characteristics are highly heritable, individual male reproductive success likely influences whether sport hunting a free-ranging population alters its evolutionary trajectory. Bighorn ram horn size is highly heritable (Coltman et al. 2003), but rams are not reproductively successful until 6-years of age with only a few males doing a majority of the breeding (Coltman et al. 2002). Selective harvest criteria that allows for removal of rams before their peak reproductive age may ultimately influence the evolutionary trajectory of a population because those rams are harvested before contributing to the gene pool (Coltman et al. 2003). In comparison, male white-tailed deer reproductive success is greatly variable because males of all ages breed (Sorin 2004, DeYoung et al. 2009, DeYoung and Miller 2011) and multiple paternity occurs in about 25% of twin litters (DeYoung et al. 2002, 2006, Sorin 2004). Therefore, harvesting male white-tailed deer of a certain antler size is less likely to alter their evolutionary trajectory.

Accounting for the maternal factors of parturition date and litter size consistently improved relationships between year-specific antler sizes and supports our prediction. The moderate predictabilities derived from the relationships between 1.5- and 2.5-year antler size and between 1.5- and 3.5-year antler size supports Lewis (2010). However, predictability nearly doubled after accounting for parturition date and litter size, suggesting that white-tailed deer are unable to compensate for the influence of maternal factors in their first 1.5-years of life.

The inability to compensate within the first year of life in response to maternal factors has been demonstrated in multiple species. For example, Knox et al. (1991) and Gray et al. (2002) found that late-born fawns grew smaller yearling antlers compared to

early-born fawns. Later parturition date also decreased weaning mass for mountain goat kids (*Oreamnos americanus;* Côté and Festa-Bianchet 2001), bighorn lambs (*Ovis canadensis*; Feder et al. 2008), white-tailed deer juvenile body mass (Michel et al. *In prep*) and 8-month-old body mass for moose (*Alces alces*; Solberg et al. 2008). Similarly, litter size negatively influenced yearling body mass in brown bears (*Ursos arctos*; Dahle et al. 2006) and fawn growth rates for roe deer (*Capreolus capreolus*; Anderson and Linnell 1997). Therefore, the negative influence of maternal factors must be considered when studying yearling morphometrics.

The influence of maternal factors decreased with increasing male age in our study. Parturition date and litter size did not improve predictability to the same extent for 2.5-year-olds as compared to yearlings, which supports Lukefahr and Jacobson (1998) who found that maternal influence on antler size was greatest for yearlings but was reduced to almost 0 as males reached maturity. White-tailed deer morphometrics may display compensation in response to negative maternal factors as these influences do not appear to negatively persist throughout an individual's life (Jacobson 1995, Michel et al. *In prep*).

Maternal factors may, however, persist for some ungulates (*Bison bison*, Green and Rothstein 1993). Green and Rothstein (1993) reported that parturition date negatively influenced multiple aspects of life such as dominance rank, body mass and fecundity and persisted for as long as 8 years for female bison. Therefore, future research should focus on identifying consistent trends related to the persistence of maternal factors as compensation may not occur for all ungulate species.

Although highly heritable, the large influence of maternal factors indicates that using yearling antler size as a selective harvest criterion may be inefficient in accomplishing management goals in populations with protracted fawning dates and variation in litter size. For example, using yearling antler size as a selective harvest criterion will not likely alter the genetic structure of a population because predictability is inefficient as parturition date and litter size are unknown to managers. Webb et al. (2012) also used simulations to show that antler size improvements were minimal for free-ranging white-tailed deer who were subjected to perfect selection based on number of antler points and concluded that using yearling antler characteristics as selective harvest criteria would not likely result in altering the genetic structure of a population. The moderate predictability of yearling antler size suggests using it for a selective harvest criterion may improve antler size of the standing crop, but managers must ensure that harvest criteria protects the largest of the yearling cohort to avoid high-grading (Strickland et al. 2001). Incorporating age as a selective harvest criterion as well as reducing hunting pressure may also increase recruitment of individuals into older-age classes (Bender and Miller 1999, Collier and Krementz 2007).

4.6 Management Implications

Using yearling antler size as a selective harvest criterion may improve antler size of the standing crop of adult animals (Demarais and Strickland 2011); however, reduction of variation associated with maternal factors will improve accuracy of predictability. Parturition date may be influenced by population demographics and nutrition. If parturition date is influenced by population demographics, then managers can reduce variation by balancing adult sex ratios which insures that females are serviced during

their first estrus (Gruver et al. 1984). Similarly, improving maternal body condition by increasing nutritional quality and quantity while reducing deer density will likely reduce parturition date variation by reducing variation in breeding dates (Cameron et al. 1992, Demarais et al. 2000). However, if parturition date is genetically determined, as for some whitetail populations (Sumners et al. 2015), then managers will not be able to reduce variation associated with parturition date. Selection efficiency will also increase if managers simply restrict selective harvest criteria for males of at least 2-years of age.

Table 4.1 Fixed and random effects for each MCMCglmm model used to estimate heritability for 2.5 through 5.5 year-old captive male white-tailed deer located near Macon, Noxubee County; Kosciusko, Attala County; Utica, Copiah County; and Morton, Scott County, Mississippi, USA, 2006–2013.

Response Variable	Fixed Effect(s)	Random Effect
Antler Score	age + generation	individual
Number of Points	age	individual
Main Beam Length[a]	age + region	individual
Inside Spread	age + region	individual
Basal Circumference[a]	age + generation	individual
Antler Mass	age + region + generation	individual

[a]Mean of both antlers

Age was used in all models to account for its known influence. Generation and region were only included in a given model if $P \leq 0.05$ in the mixed model of variance.

Table 4.2 Age-specific mean antler score for captive male white-tailed deer located near Macon, Noxubee County; Kosciusko, Attala County; Utica, Copiah County; and Morton, Scott County, Mississippi, USA, 2006–2013.

Age (years)	*n*	Mean Antler Score (cm)	Number of Points	Main Beam Length[a] (cm)	Inside Spread (cm)	Basal Circumference[a] (cm)	Antler Mass (g)
1.5	107	91.3 ± 51.6	4.1 ± 2.1	19.9 ± 9.2	16.1 ± 7.1	6.0 ± 1.2	121.1 ± 94.43
2.5	97	214.1 ± 50.7	7.5 ± 1.4	39.0 ± 6.8	32.1 ± 6.3	8.6 ± 1.3	472.0 ± 207.7
3.5	87	271.8 ± 52.6	8.3 ± 1.4	46.7 ± 8.3	36.7 ± 6.5	10.4 ± 1.5	791.3 ± 325.5
4.5	28	280.2 ± 54.9	8.0 ± 0.8	47. 7 ± 9.4	38.0 ± 4.9	10.1 ± 1.1	794.0 ± 353.2
5.5	6	294.3 ± 28.3	7.6 ± 0.5	51.7 ± 4.9	41.7 ± 7.9	11.1 ± 1.1	-

[a]Mean of both antlers

Antler sets were unavailable for weight for 5.5-year-olds. Mean ± SD.

Table 4.3 Heritability estimates and associated 95% Credible Intervals for 2.5- through 5.5- year-old captive male white-tailed deer located near Macon, Noxubee County; Kosciusko, Attala County; Utica, Copiah County; and Morton, Scott County, Mississippi, USA, 2006–2013.

Trait	h^2	95% *CI*
Antler Score	0.84	0.77 - 0.89
Number of Points	0.63	0.49 - 0.74
Main Beam Length[a]	0.78	0.69 - 0.81
Inside Spread	0.72	0.61 - 0.80
Basal Circumference[a]	0.75	0.63 - 0.81
Antler Mass	0.72	0.61 - 0.80

[a]Mean of both antlers

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APPENDIX A

SUMMARIES OF INDEPENDENCE CLAIMS AND NULL PROBABILITIES

Table A.1 Tests of conditional independence of the basis sets implied by the path model of the direct early life characteristics model represented in Figs. 2–4.

Independence Claim	t value	Null Probability (p_i)
Yearling		
1_||_7|{4,6}	-2.098	0.043
1_||_8|{4,6}	-0.403	0.690
2_||_7|{1,4,5,6}	1.694	0.098
2_||_8|{1,4,5,6}	0.755	0.455
3_||_7|{1,2,4,5,6}	0.352	0.727
3_||_8|{1,2,4,5,6}	0.198	0.844
5_||_7|{1,4,6}	0.404	0.690
5_||_8|{1,4,6}	-1.132	0.267
7_||_8)|{4,6}	0.539	0.593
Two-Years		
1_||_7|{4,6}	-0.059	0.953
1_||_8|{4,6}	0.724	0.474
2_||_7|{1,4,5,6}	1.605	0.117
2_||_8|{1,4,5,6}	1.402	0.174
3_||_7|{1,2,4,5,6}	1.071	0.292
3_||_8|{1,2,4,5,6}	0.984	0.332
5_||_7|{1,4,6}	1.436	0.160
5_||_8|{1,4,6}	0.870	0.393
7_||_8|{4,6}	2.276	0.033
Three-Years		
1_||_7|{4,6}	-0.342	0.735
1_||_8|{4,6}	0.856	0.398
2_||_7|{1,4,5,6}	2.001	0.054
2_||_8|{1,4,5,6}	1.061	0.297
3_||_7|{1,2,4,5,6}	1.835	0.077
3_||_8|{1,2,4,5,6}	0.741	0.464
5_||_7|{1,4,6}	2.001	0.054
5_||_8|{1,4,6}	0.753	0.460
7_||_8|{4,6}	0.685	0.498

Variables: 1 (age), 2 (maternal body mass), 3 (offspring birth mass), 4 (juvenile body mass), 5 (cumulative lactation demand), 6 (birth date), 7 (adult body mass), 8 (adult antler size).